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Amphibians in Complex Landscapes: Quantifying Habitat Connectivity for Juvenile Movements and Dispersal

Brittany Blue Cline

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**AMPHIBIANS IN COMPLEX LANDSCAPES: QUANTIFYING HABITAT
CONNECTIVITY FOR JUVENILE MOVEMENTS
AND DISPERSAL**

By

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A DISSERTATION

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Doctor of Philosophy

(in Wildlife Ecology)

The Graduate School

The University of Maine

August 2014

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August 4, 2014

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AND DISPERSAL**

By Brittany Blue Cline

Dissertation Advisor: Dr. Malcolm L. Hunter, Jr.

An Abstract of the Dissertation Presented
in Partial Fulfillment of the Requirements for the
Degree of Doctor of Philosophy
(in Wildlife Ecology)
August 2014

Maintaining amphibian populations in fragmented landscapes depends on preserving functional connectivity for animals that need to transit multiple vegetation types to satisfy habitat requirements. For many pool-breeding amphibians, successful dispersal is essential for gene flow; thus, quantifying the ability of juveniles to locate and reach suitable habitat in the terrestrial matrix is necessary to predict the consequences of landscape configuration for populations. I evaluated if different open-canopy vegetation types alter the behavior of juvenile wood frogs (*Lithobates sylvaticus*). First, I quantified the relative permeability of different open-vegetation types by experimentally releasing frogs in 35 x 3 m enclosures extending from forest edge into five treatments. Based on an index that compounds four metrics and scales relative to mature forest, permeability varied: row crop < hayfield < clearcut < open lawn < moderate-cover lawn. Results indicated that juveniles may make forays into the open, assess habitat, and change directionality. Second, I tested juvenile orientation at silvicultural edges in heavy partial harvests (31-

60% retention). Overall, a slightly greater, statistically insignificant, percentage of individuals entered control; harvester trails running perpendicular to the edge of uncut forest may represent a partial filter to movements. Finally, I quantified the fine-scale movements of individuals released on five substrates (asphalt, corn, forest leaf litter, hay, lawn), and the directionality of frogs released at different distances from forest using fluorescent-powder tracking. Movement performance differed: frogs demonstrated straighter paths, and greater net movements, path lengths and velocities through treatments with lower structural complexity. Frogs exhibited directionality toward forest in asphalt, lawn, and corn, indicating that differing characteristics of the non-forest matrix may influence the ability of frogs to traverse open cover and orient toward forest from distances of 40-55m. Differences in the willingness of animals to enter treatments, coupled with motility and residency times, support the differing roles of open-canopy vegetation as filters and conduits to movement. Thus, it may be overly simplistic to estimate matrix permeability as uniformly low in models that predict movement in fragmented landscapes. To promote functional connectivity, modification of vegetation composition and configuration may provide an underutilized tool for conservation practitioners to reduce the effective isolation of habitat patches for post-metamorphic amphibians.

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CHAPTER 1

DIFFERENT OPEN-CANOPY VEGETATION TYPES AFFECT

MATRIX PERMEABILITY FOR A DISPERSING

FOREST AMPHIBIAN

Abstract

Population viability often depends on conserving functional connectivity in fragmented landscapes. For pool-breeding amphibians, population connectivity is largely maintained through juvenile dispersal, often through various vegetation types that may differ as filters or conduits to movement. We quantified the relative permeability of different types of open-canopy vegetation to juvenile wood frogs (*Lithobates sylvaticus*) to determine if this influences functional connectivity during dispersal. We conducted experimental releases of juveniles (n = 561) in ten runways representing five treatments: hayfield; moderate-cover lawn (45–85% cover); open lawn (0% cover); row crop (forage-corn); and recent clearcut. Runways consisted of 35 x 2.5 m enclosures, located perpendicular to a forest edge and extending into treatment areas with tracking stations at 10, 20 and 30 m. As indices of permeability, we measured the number of animals traversing each station, the proportion changing direction, movement timing, and movement rates. Based on an index that compounds four metrics and scales them relative to mature forest as a control, permeability varied among open-canopy cover types in the following order: row crop < hayfield < clearcut < open lawn < moderate-cover lawn. The highest proportions of individuals changed direction (toward forest) in the hayfield, moderate-cover lawn, and clearcut, suggesting that juveniles may make forays

into the open and subsequently assess habitat. Nonetheless, individuals could eventually transit entire runways, indicated by overall recaptures at 30 m (e.g. hayfield, 29%; moderate-cover lawn, 24%; and clearcut, 20%) at the end of our six-week experiment. We provide quantitative evidence that open-canopy cover types may act as differential ecological filters to ranging movements, and ultimately dispersal. Differences in the willingness of animals to enter treatments, coupled with motility and residency times, support the differing roles of open-canopy vegetation as both filters and conduits to movement. Thus, it may be overly simplistic to estimate matrix permeability as uniformly low in models that predict movement in fragmented landscapes. To promote functional connectivity, modification of vegetation composition and configuration may provide an underutilized tool for conservation practitioners to reduce the effective isolation of habitat patches for post-metamorphic amphibians.

Introduction

For many species, quantifying functional connectivity among preferred habitats is critical for understanding the mechanisms that drive long-term population persistence in fragmented landscapes (Revilla et al., 2004; Van Buskirk, 2012). It is widely recognized that population viability is maintained by dispersal among breeding sites (Hudgens et al., 2012), and further, that successful dispersal depends on the characteristics of the matrix that intervenes between suitable habitats and the interaction of landscape structure with species-specific behavior (Burgess et al., 2012). Despite this critical relationship, conventional assumptions of patch-matrix models often oversimplify the matrix of non-preferred habitats as singularly unsuitable (Kuefler et al., 2010). In reality, the type of

matrix may influence the probability of an animal entering the matrix, the speed of movement, and ultimate dispersal success. Researchers increasingly acknowledge that there are grades of matrix condition that differ as filters or conduits for movement (Zeller et al., 2012). However, quantifying this variation in matrix permeability (or conversely, resistance) remains a fundamental challenge. Furthermore, some species might prefer matrix conditions during dispersal even though they differ from preferred conditions for settlement. In this context, it would make sense to refer to “dispersal habitat” and “breeding habitat” instead of a matrix of non-habitat interspersed by patches of suitable habitat.

The accelerating conversion of natural ecosystems to human-dominated land cover (Desrochers et al., 2011) heightens the need to consider diverse cover types that may constitute dispersal habitat. It is possible that for some species human-determined open-canopy cover types may be acceptable for dispersal (i.e., low travel costs) and thus maintain functional connectivity. In particular, Kuefler and colleagues (2010) have pointed out that deterrents to movement at boundaries (e.g., perceived risks of entering an open-canopy cover type due to predation) might be mitigated by faster locomotion after these edges are crossed. Furthermore, animals of the same species may prefer different vegetation types for movements depending on the behavioral context (e.g., risk of predation versus thermal stress in a particular time or place). There is need to quantify vegetation-type specific movement and boundary behaviors.

Amphibians are appropriate taxa for studying this issue because their movements are typically at tractable scales and because many species rely on aquatic and terrestrial habitat connectivity. In particular, juveniles typically emerge into the terrestrial

environment from their natal pool soon after metamorphosis, sometimes emigrating to a new breeding pool (dispersal) and sometimes returning to breed in their natal pool (philopatry). Both dispersing and philopatric juveniles may need to transit heterogeneous vegetation, but dispersers are likely to cover greater distances and be more likely to encounter diverse vegetation (Clobert et al., 2009).

Most permeability studies have relied on expert-derived estimates for models and simulations of structural and functional connectivity (e.g., Hudgens et al., 2012). Some studies have quantified the relative permeability of habitats to juvenile amphibians, especially in forests (e.g., Rothermel and Semlitsch, 2002; Rittenhouse and Semlitsch, 2006), but none have directly measured the permeability of different open-canopy cover types. Prior dispersal research in agricultural, recreational (e.g., golf course), or urbanizing landscapes has focused on individual orientation (Vos et al., 2007), landscape and site-specific factors affecting occupancy (Revilla et al., 2004), or resistance of the matrix to gene flow (Van Buskirk, 2012). If habitat permeability declines for forest amphibians after timber harvest, at least temporarily (Semlitsch et al., 2008), it is reasonable to presume that the conversion of forest to agricultural or suburban lands might reduce functional connectivity.

Study species and goal

In this study, we quantified the relative permeability of open-canopy cover types to juvenile wood frogs (*Lithobates sylvaticus*) during the post-metamorphic period when they leave natal pools. They are highly sensitive to forest removal and avoid proximity to forest edges (deMaynadier and Hunter, 1998). Dispersal success (i.e., juveniles surviving

to breed in new sites) has been estimated at 18–20% (Berven and Grudzien, 1990).

Dispersal distances have been recorded at > 1000 m (females: 1140 ± 324 m; males: 1276 ± 435 m), with a maximum of 2530 m (Semlitsch and Bodie, 2003). The scale of overland movements may make this species particularly vulnerable to loss of connectivity.

We undertook experiments on the movements of juvenile *L. sylvaticus* in open-canopy cover as an extension of a prior study on movements through forestry treatments (Popescu and Hunter, 2011). Our goal was to document movement patterns through five types of open-canopy vegetation resulting from forest (clearcutting), suburban (open-canopy and moderate-cover lawns), and agricultural (row crop, hayfield) practices. Our guiding hypothesis was that these open-canopy cover types differ as filters or conduits for dispersal. In the next section, we describe how movement behavior leads to dispersal. Then, we develop a predictive framework for permeability (or conversely, resistance), in which we specify *a priori* hypotheses about differences in post-metamorphic movements among treatments.

Post-metamorphic movements

Increasingly, animal ecologists employ a behavioral landscape view in which movement is an adaptation to spatiotemporal variation in resource distribution (Bélisle, 2005). As such, dispersal movement is shaped both by external factors and individual traits, including morphological, life history-based, behavioral, or physiological attributes, often likened to a dispersal “syndrome” (Clobert et al., 2009). To conceptualize post-metamorphic movement of *L. sylvaticus*, we first recognize two types of movement,

based on Dingle (1996), which can be construed as opposite ends of a continuum. Migration movements tend to be toward distant resources and are not directly responsive to proximate resources (e.g., Dingle and Drake, 2007; Pittman et al., 2014). For example, annual journeys of adult wood frogs from hibernaculum to breeding pools are migrations primarily because they are directed toward breeding sites and not resources along the route. In contrast, movements that are directed toward an animal's need for immediate resources are termed "station-keeping;" seeking a suitable microclimate is an example. An intermediate form of movement is "ranging," in which an individual departs from a location, travels moderate distances seeking resources, and occupies the first suitable patch of habitat encountered. We speculate that post-metamorphic frogs are largely driven by "ranging," in which individuals leave their natal pool, make exploratory movements seeking food and an appropriate microclimate, and cease when suitable habitat is found (Bowler and Benton, 2005). Over time, ranging movements that are relatively long or repeated may ultimately lead to dispersal to a new breeding pool; shorter ranging movements may result in philopatry. The exploratory nature of ranging suggests that movements may be highly influenced by the ability of individuals to detect environmental conditions from some distance and move toward or away from them. Key environmental factors probably include vegetation structure, microclimate, food, predators, and conspecifics.

A predictive framework for permeability

At the study outset, we predicted that several factors might influence the observed patterns of permeability, or resistance. We defined permeability and resistance as broad,

converse measures of the degree to which the vegetation (or larger landscape) either facilitates or impedes (respectively) an organism's movement between resources or preferred habitat patches (e.g., Bélisle, 2005). Broadly, we predicted that movements would be facilitated (i.e. more willingness to enter or traverse greater distances at greater velocities) through vegetation that was more similar to forest, the species' terrestrial settling habitat (Eycott et al., 2012). Prior studies indicate that amphibians modify movements (e.g. velocity, latency, path tortuosity, willingness to enter habitats) in response to ground substrate, habitat extent (Rothermel and Semlitsch, 2002), vegetation structure, microclimate (Rittenhouse et al., 2008), and physiological factors such as stress-hormone levels (Janin et al., 2012).

Specifically, we predicted that the most open and least structurally complex cover types (open lawn, row crop) would be less permeable than types with greater canopy cover and structural complexity (moderate-cover lawn, hayfield, and clearcut). Permeability in this context has three key elements that we can measure, which depend on the interaction between individual behavior and vegetation structure: (1) willingness to enter a vegetation type; (2) probability of crossing the vegetation type; and (3) velocity. There are some likely trade-offs between the factors that collectively influence movement success. For example, a frog may be more willing to enter dense vegetation with a lower risk of desiccation even though thick vegetation will impede its velocity and thus increase the time it is outside the forest.

Recognizing these trade-offs, we predicted that frogs in open lawns or row crops would: (1) demonstrate low willingness to enter; (2) traverse only short distances; and (3) move faster, compared to moderate-cover lawns, hayfields, or clearcuts. More

specifically, we expected to observe a greater proportion of animals returning to the nearest forest edge when released in our most open treatments (lawns or cornfields), while a greater proportion of animals would be recaptured or tracked at distances extending into hayfields or clearcuts, where increased habitat structure might afford cool moist microclimates or cover from predators. However, we also predicted high movement rates for (and large distances traversed by) the proportion of animals venturing into cornfields and lawns, if simplified vegetation structure represented low impedance for locomotion. Finally, we predicted that the timing of movements in hayfield and clearcut might be protracted if locomotion was slow due to thick ground vegetation and individuals perceived these treatments as a refuge with suitable microclimates and lower predation risk.

Materials and Methods

Study sites and experimental design

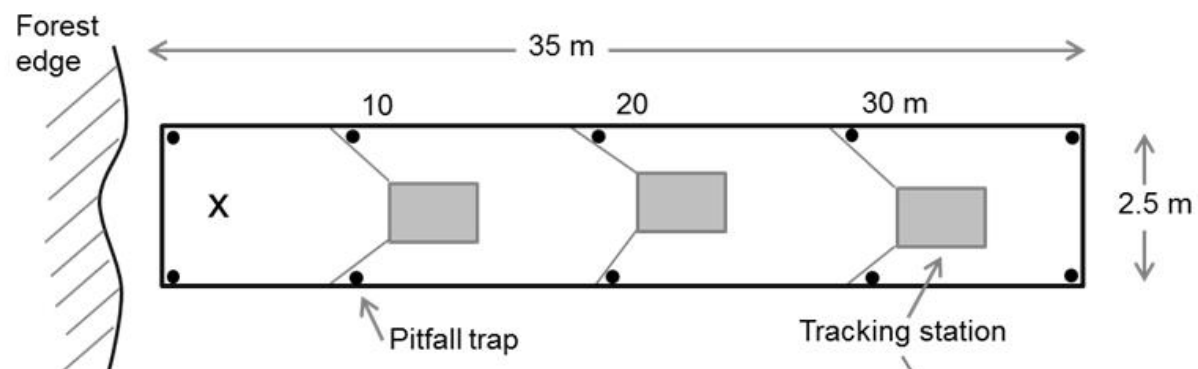
We conducted this experiment in Penobscot County, Maine, USA on lands managed by the University of Maine's Agricultural and Forest Experiment Station (MAFES). Extensive forest management in the Acadian Forest region has generated a mosaic of mixed-wood stands of various age classes. Our study area is in the lower Penobscot River watershed (9,974 km²), where 78.3% of the landscape is forested (of which 20.4% has recently been cut), 3.9% is urban, 3.9% is agriculture, and the balance is water bodies and wetlands. We selected five open-canopy treatments that typify the region: (1) hayfield; (2) moderate-cover lawn (~ 45–85% cover by ornamental trees); (3) open lawn (0% cover); (4) row crop (silage corn); and (5) recent clearcut (3–5 years).

The hayfield constituted a mixture of grasses and legumes, with average stem height of 0.87 m; baling occurred on 23 July 2010, but a continuous swath of hay was retained within and between treatments and extending > 10 m in all directions from edges. The lawn treatments (hereafter, open lawn or moderate-cover lawn) comprised exotic grasses; no mowing occurred during the study (7 July – 5 August 2010). The row crop treatment (hereafter, cornfield) comprised feed corn, sown in late May. The inter-row distance averaged 1.1 m (range: 0.40–2.58 m). The forest clearcut (hereafter, clearcut) was characterized by complete overstory removal (0% canopy cover), an herbaceous stratum < 50 cm, and lacked tree regeneration.

Experimental runways

Runways were a modification of the design of Popescu and Hunter (2011): 35 x 2.5 m silt-fence enclosures (60 cm height; 15–20 cm into ground). Our experimental units constituted individual batches of frogs (released in six batches over six weeks), nested within five treatments and ten runways (two per treatment). Each runway was located along a perpendicular edge between closed-canopy forest (not harvested in > 20 yrs) and each treatment. Location of each runway along the edge was selected randomly and 35–50 m from its replicate. Inside each runway, we constructed three identical tracking stations at 10, 20, and 30 m from the forest edge. Tracking stations constituted plastic containers (45 x 65 x 20 cm), placed in the mouth of a silt-fence funnel (Figure 1.1). Each station sheltered two pieces of paper: a waterproof paper coated in a mix of mineral oil and orange fluorescent powder, placed just in advance of a white sheet of paper (20.3 x 43.2 cm). Frogs passing through stations would leave their tracks

Figure 1.1. Experimental design for evaluating the permeability of five open-canopy cover types to juvenile wood frogs *Lithobates sylvaticus* during post-metamorphic dispersal. The top panel depicts four of the five treatments tested: (a) hayfield; (b) lawn (two treatments: 0%; 45–85% cover); (c) row crop (feed corn); and (d) clearcut. The middle panel illustrates tracking station design; **x** indicates initial release (drawing not to scale; adapted from Popescu and Hunter, 2011). The bottom panel depicts fluorescent-powder tracks; the arrow denotes runway directionality.



on the white paper; the 20-cm height of the box ensured that frogs could not jump over stations. Each sheet was changed daily, and we employed double-observer methods to record the unidirectional passages of individuals through stations.

Each runway contained 10 pitfall traps (Figure 1.1): two at the start and two at the end, and two at the junction of each silt-fence funnel and runway wall. We used pitfalls to estimate the number of individuals reaching the end of runways (35 m, i.e., indicative of open-cover permeability), versus returning to the edge (0 m) or changing movement direction (10 or 20 m), all indicative of open-cover avoidance.

Juvenile amphibian rearing and release

We collected *L. sylvaticus* egg masses from the University of Maine's Penobscot Experimental Forest, Maine, USA and raised these in plastic wading pools at a forested site until hatching. When larvae reached Gosner (1960) stages 21–23, we moved them to 1500-L cattle tanks (80 per tank) established as semi-natural mesocosms. At larval stages ≥ 42 , individuals were moved into large plastic bins (200-L, lined with moist leaf litter) until metamorphosis (Gosner stage 47). Prior to each release, we measured (snout-vent length: SVL), marked (single toe clip per batch), and randomly assigned frogs to treatments. We released 561 *L. sylvaticus* across six batches. Within each runway, we released 7–12 animals per batch (consistent within batches). Frogs were released 5.5 m from forest edge in the center of each runway (~ 2.5 m from the side walls) 1–2 hours after sunset; we released a subsequent batch only after track sheets denoted no new tracks (≥ 1 day). By waiting 3–6 days before beginning a new batch, most frogs from prior releases had been recaptured or had moved beyond the first runway compartment

(minimizing the possibility of density-dependent effects; e.g., Patrick et al., 2008).

Runways were monitored 06:30–11:00 h (9 July – 7 August 2010).

Microhabitat and microclimate variables

We collected temperature, relative humidity, and daily precipitation in our five treatments using 26 iButton data loggers (Maxim, Inc., Dallas Texas, USA). In the middle compartment of each runway (10–20 m), we measured hourly temperature at: (1) ground-level; (2) under refugia (i.e. 5–8 cm below coarse woody material in clearcut, under root masses in hayfield, etc.); and (3) 120 cm above ground in shade. We also measured (4) relative humidity (ground-level). Refugia temperatures were not obtained in lawn treatments due to lack of microcover. We also collected microhabitat data, characterizing vegetation in terms of ground cover, canopy closure, vegetation height, stem density, and inter-row distance. Habitat characteristics of the hayfield, cornfield, and lawn were collected on 16, 22, and 29 July 2010 to account for vegetation growth.

Statistical analyses

Our experimental design generated four indices to quantify permeability of treatments: (1) the proportion of tracks at each station (10, 20, and 30 m); (2) the proportion of animals captured in pitfall traps; (3) movement timing; and (4) movement rate. The first two metrics indicate an individual's willingness to enter a given treatment; the third and fourth metrics are joint estimates of velocity within that cover type. All four metrics collectively comprise a measure of cover-type permeability.

For the first index, our dependent variable was the proportion of frogs that reach each station (using tracks to infer the number of single passages of individuals) out of the total released per runway. We assessed whether (a) treatment; (b) individual runway; or (c) batch affected the number of tracks recorded (10, 20, and 30 m from forest edge) using our observed values, generalized linear mixed-effects models (GLME), and generalized linear models (GLM). Thus, we ran models for each distance (10, 20, and 30 m) to avoid autocorrelation (i.e., the same individuals counted in successive stations). Appendix A in Supporting Information provides our model methods and results.

We analysed our second index (i.e., the proportion of animals recaptured among treatments) by distance classes (0, 10, 20, and 30–35 m), using three-way contingency tables and pairwise tests for proportions. We quantified this as the proportion of juveniles that were recaptured at each distance (0, 10, 20, and 30–35 m), out of the total reaching each station (from track-counts; index #1). Because the pitfall traps at 30 and 35 m were located in the same compartment (Figure 1.1), we pooled their data. Further, the number of animals captured within the 0 m and 30–35 m classes was compared to the total number of released for that runway. We evaluated the relationship between capture frequency and distance, testing for non-independence. We employed pairwise tests for proportions and chi-square tests to estimate differences in capture frequency between treatments at each distance.

Finally, we evaluated potential differences in movement timing and rate (indices #3–4, or velocity). First, we evaluated movement timing 1–5 days following release using the number of tracks in each station as a proportion of the total number of tracks recorded per runway. We only used data from juveniles ($n = 54$) captured past the first

(10 m) station. We evaluated potential differences in timing between treatments using a non-parametric (chi-squared) Kruskal-Wallis test for proportions (R package [coin]; Hothorn et al., 2008). Secondly, we evaluated velocity in each treatment (m day^{-1}) using data from 294 individuals that were tracked past the first stations. We used total track counts (i.e., the series of tracks comprising the passage of a single individual through 10, 20 or 30 m stations) to determine the total minimum distance traversed across the entire experiment (this constituted 4740 total m in 10 runways and 27 tracking days, and did not represent a single individual's passage through consecutive stations). We then pooled distances by treatment to obtain average rates (i.e., the total number of m traversed in each treatment divided by the number of days during which movement occurred), and investigated potential differences among treatments using a one-way analysis of variance (ANOVA, R package [car]; Fox and Weisberg, 2011). We modeled rate (m day^{-1}) as a correlate of the willingness of individuals to enter using a simple linear regression model (Pearson's linear correlation coefficient r). We parameterized willingness to enter using the observed proportion recaptured at 10, 20, or 30–35 m (but not those that demonstrated avoidance at 0 m), out of the total released in that treatment.

We computed a composite index of permeability that incorporated all four movement metrics, giving equal weight to each. We assumed that juvenile wood frog movements would be facilitated (i.e., have highest permeability values) through mature forest (i.e., terrestrial settling habitat) based on Popescu and Hunter (2011) and thus used their results (obtained using the same methodology and species in the same locale) as a benchmark of permeability. See Appendix B.

We assessed potential differences in the size of metamorphs (SVL) released among treatments using a one-way analysis of variance (ANOVA; program R, version 2.13.2). All statistical tests were deemed significant at $P < 0.05$.

Results

We quantified differences in the relative permeabilities of open-canopy types (hayfields, lawns, row crops, and clearcuts) to juvenile *L. sylvaticus* during post-metamorphosis using four metrics of movement as described in the next three sections. An index derived from these four metrics suggested the following order of permeability (lowest to highest): **1.** row crop (0.40); **2.** hayfield (0.47); **3.** forest clearcut (0.55); **4.** open lawn (0.58); and **5.** moderate-cover lawn (0.67; see Appendix B). Across treatments and experimental releases (batches), the average size (SVL) of juveniles was 16.2 ± 1.1 mm, with no differences among treatments (ANOVA; $F_{4, 176} = 1.57$, $P = 0.183$).

Willingness to enter: Proportion of animals reaching tracking stations

Across the five treatments, the number of frog tracks recorded differed at all distances (Figure 1.2), indicating an effect of cover type on the willingness of frogs to enter a given treatment (e.g., ANOVA for 10-m track model predictions; $F_{4, 59} = 2.73$, $P = 0.03$). The proportion of tracks was consistently highest in the cornfield and the moderate-cover lawn, while the hayfield was the least permeable (ANOVA for 30-m model predictions; $F_{4, 49} = 2.25$, $P = 0.07$; Figure 1.2). The clearcut and open lawn results were consistently similar and intermediate (observed proportions and model predictions;

Figure 1.2, Appendix A). Using the proportion of animals reaching 30 m to infer movement success, the cornfield was 5.3 and 8.4 times more permeable than the open lawn and hayfield, respectively, while the moderate-cover lawn was 5.9 times more permeable than the hayfield.

Willingness to enter: Proportion of recaptures

We released 561 juvenile frogs and recaptured 349 (62.2%) across treatments and runways (Table 1.1). Recapture rates ranged from 37.7% (hayfield) to 80.7% (cornfield), with intermediate rates in the clearcut (49.5%), moderate-cover lawn (69.6%), and open lawn (73.2%).

Classified by distance (0, 10, 20, and 30–35 m), the percentage of captures varied by treatment ($\chi^2_{12} = 92.6$, $P < 0.001$) indicating an effect of cover type on the willingness of frogs to enter. The majority of recaptures occurred at 0 m in the cornfield (68%), lawns (open and moderate-cover; 64% and 51% respectively), and clearcut (47%), indicating a propensity for individuals to return to the forest (Table 1.1 and Figure 1.3). The hayfield results contrasted sharply; among treatments, it had the lowest overall recapture rate at 0 m (33%), and the highest rate for all other distances (Table 1.1). Thus, frogs in the hayfield were significantly less likely to move toward the edge (i.e., 0 m) compared to the cornfield ($P < 0.001$) and open lawn ($P < 0.001$). Furthermore, once in the hayfield, a significantly greater percentage (29%) travelled the entire runway (35 m) compared to the cornfield ($P = 0.002$; Figure 1.3). The percentage of frogs traveling the entire runway was also high in the moderate-cover lawn (24%), yet recapture rates were

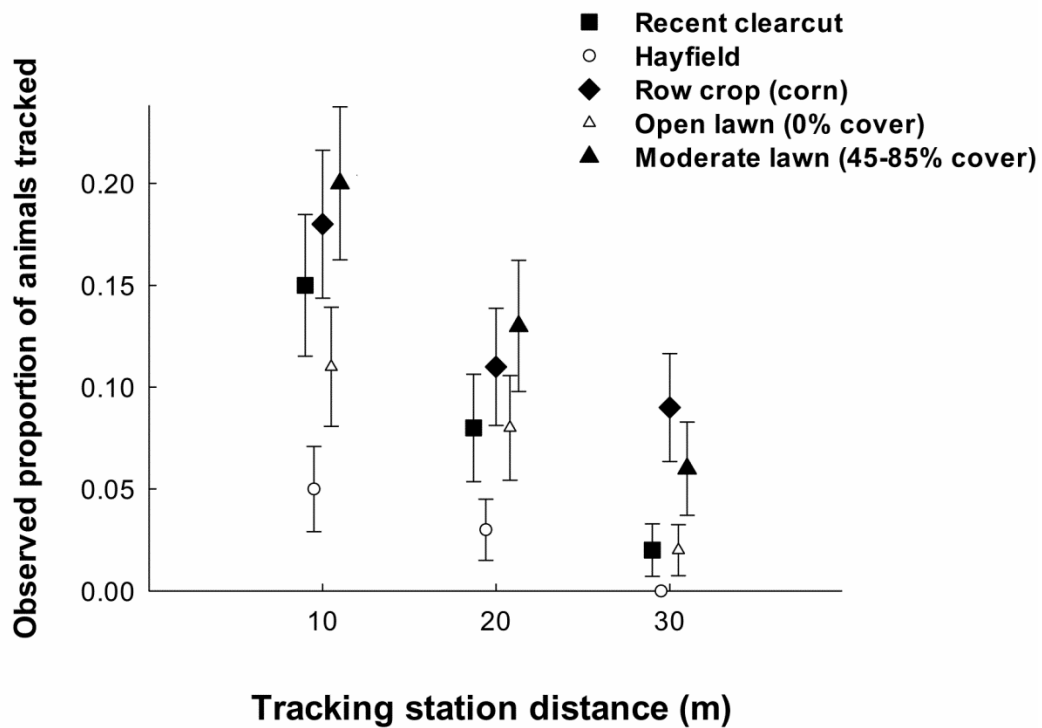


Figure 1.2. Observed proportions of juvenile *L. sylvaticus* reaching: (a) 10-m; (b) 20-m; and (c) 30-m tracking stations in five open-cover types (mean \pm SE). Values on y-axis are observed proportions of released individuals moving through stations averaged across runways and batches (mean \pm 1 SE).

relatively low at 35 m in the cornfield (7%) and open lawn (10%, Figure 1.3; Table 1.1), where ground vegetation structure was simple, but canopy was largely absent.

The distribution of recaptures at intermediate stations (10 and 20 m) is noteworthy because they indicate animals changing directionality after entering a treatment (Figure 1.3). Higher percentages of individuals were recaptured at 10 m in the hayfield (67%) and lawn (open 42%; moderate-cover 36%) than in the clearcut (6%) and cornfield (24%, Table 1.1). At 20 m, the hayfield maintained the highest capture rate (33%); in contrast, the most exposed cover types (open lawn, cornfield) had the lowest recaptures (8% and 11%, respectively).

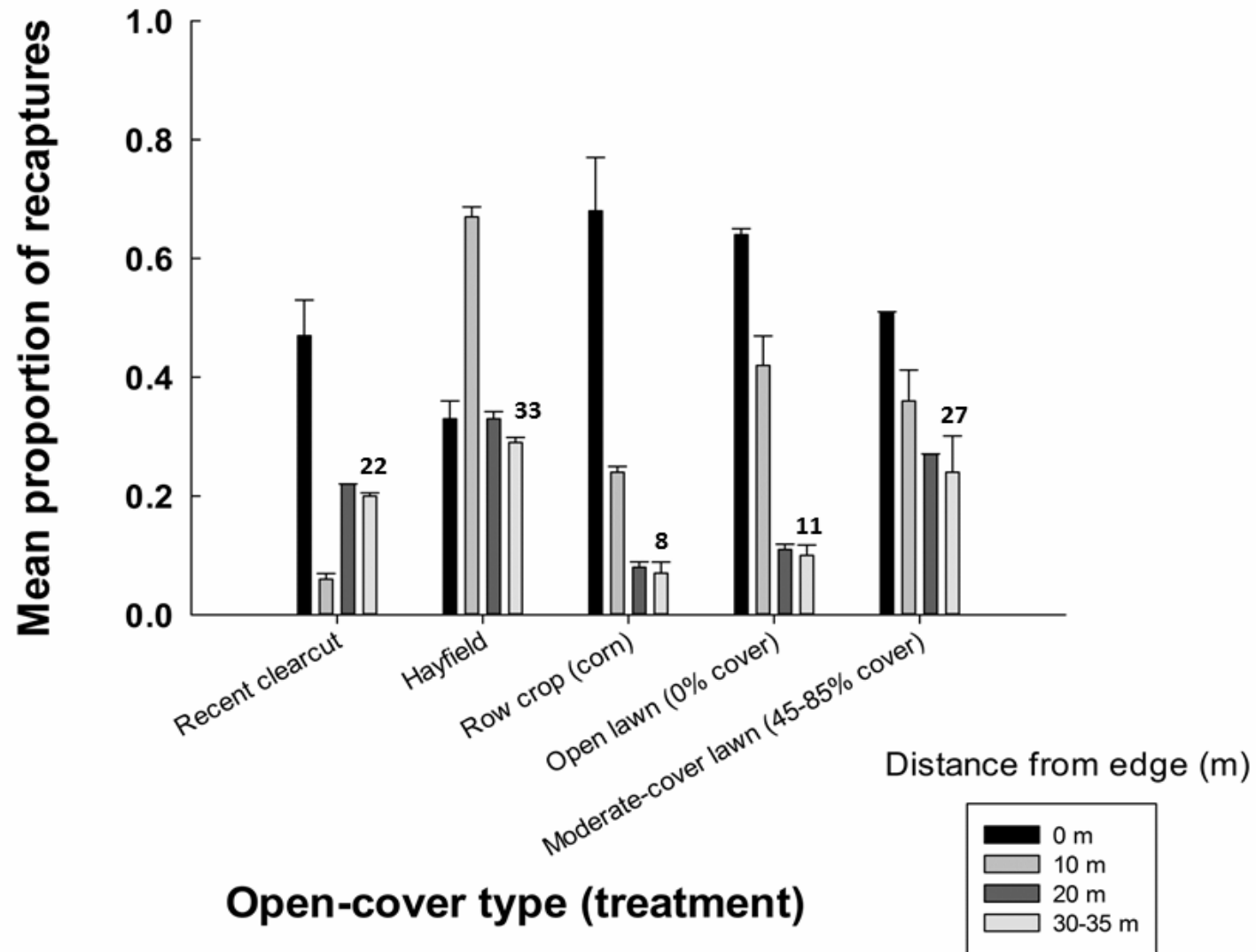
Table 1.1. Percentage (%) of juvenile wood frogs *Lithobates sylvaticus* recaptured in experimental runways, categorized by five open-canopy cover type (treatments) in 2010, and 2 reference treatments (forest clearcut and mature forest) in 2008–09.

Open-canopy cover type (treatment)	No. juveniles released	Individuals recaptured (%), by tracking distance (m)			
		0 m	10 m	20 m	30 and 35 m (2010) 40 and 50 m (2008–09)
2010 recapture	349 (561)				
Forest clearcut*	109	47 ^A	6	22	20
Hayfield	114	33 ^B	67	33	29 ^A
Row crop (feed corn)	114	68 ^{AB}	24	8	7 ^{AB}
Lawn (0% cover)	112	64 ^B	42	11	10 ^A
Lawn (~45–85% cover)	112	51 ^B	36	27	24 ^B
2009 recapture					
Forest clearcut*	118	48	24	5	7
Mature forest	117	18	11	0	31
2008 recapture					
Forest clearcut*	112	30	23	13	11
Mature forest	133	19	5	0	29

* Forest clearcut treatments comprise the same experimental runways and sites across both studies (2008–10)

Notes: Observed values at 10 and 20 m represent the number of individuals recaptured relative to the number of animals that reached those respective distances; thus sums across rows do not equal 100%. Superscript letters (A, B) identify similarity or dissimilarity among treatments for each distance, based on pairwise tests for proportions. Recapture sample sizes at 10 and 20 m distances were too small for statistical analysis; similarly, 2008–09 reference data were not analysed (see Table 1 in Popescu & Hunter 2011).

Figure 1.3. Proportion of juvenile *L. sylvaticus* reversing movement direction in runways, categorized by five treatments and four distances. Values on the y-axis are observed proportions of released animals that were recaptured in pitfall traps (mean \pm 1 SE, across runways and batches) at four distances (0, 10, 20, 30–35 m). Recaptures at 0 m indicate low matrix permeability (high resistance); at 35 m indicate high permeability (low resistance), and at intermediate stations denote a change in direction (forest edge). Percentage values indicate the proportion of individuals reaching 35 m out of total released for each treatment (n = 109–114).



Velocity: Movement rates and timing of movements

Across all treatments, we obtained movement rates for 294 individuals recaptured past 10 m (which collectively traversed 4740 m during the 27-day experiment). Average movement rates ranged between 8.9 and 55.6 m day⁻¹ (Figure 1.4), and differed significantly by cover-type (ANOVA; $F_{4,5} = 199.5$, $P < 0.001$). We observed highest motility in the open and moderate-cover lawn treatments (55.6 and 54.1 m day⁻¹, respectively), and lower rates in the clearcut (30.4 m day⁻¹), cornfield (26.7 m day⁻¹), and hayfield (8.9 m day⁻¹; Figure 1.4). There was a strong negative relationship between the observed proportion of juveniles entering a treatment and the movement rate within that treatment (Figure 1.4; $R^2 = 0.44$; $r = -0.66$; d.f. = 4; $P < 0.01$). For example, the hayfield represented the least permeable treatment according to velocity (8.9 m day⁻¹); yet, we observed the highest proportion of released frogs enter this cover type (0.68 out of total released; Figure 1.4).

Most movements occurred within the first 3 days post-release, but within this period we found differences in the timing of movements by treatment (Figure 1.5a–c). Individuals in the cornfield, clearcut, and moderate-cover lawn made the earliest (and longest) forays into runways, while the hayfield and open lawn were permeated slowly (only 5.3% reaching 20 m in the hayfield by day 3; Figure 1.5a–c). Across all treatments (and on average), 7.5% reached 30 m. Juveniles moved quickly once a direction was selected, with the exception of the hayfield (Figure 1.5c). The majority of recaptures occurred within the first three days post-release (91%) with only 33 animals spending > 3 days in runways (12: hayfield; 10: cornfield; 6: moderate-cover lawn; 4: open lawn; 1: forest clearcut).

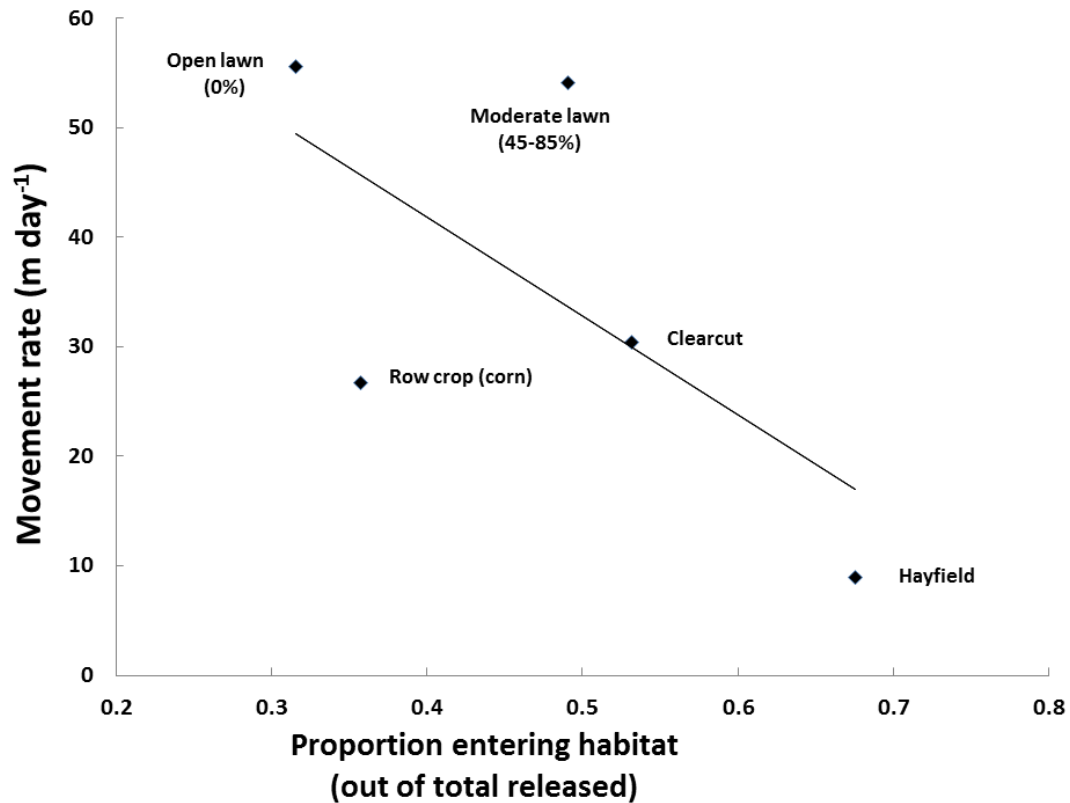


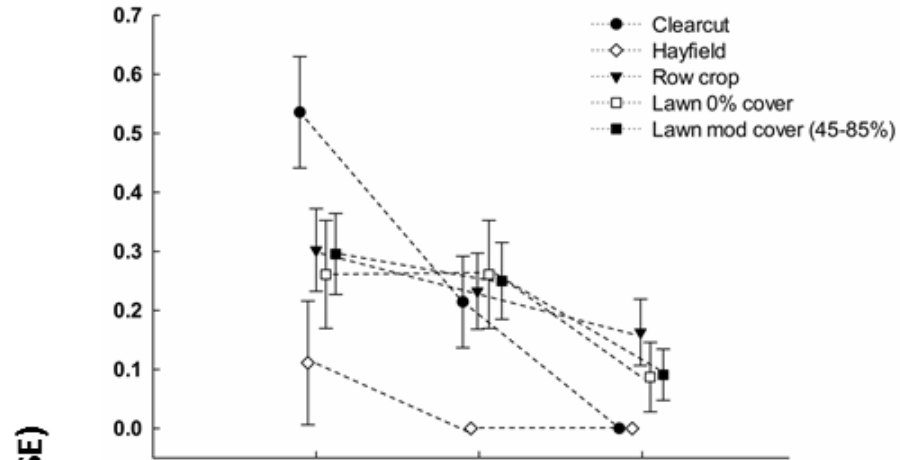
Figure 1.4. Relationship between the observed proportion of juvenile *L. sylvaticus* entering a treatment and movement rate within that treatment. The observed proportion entering a treatment is the proportion recaptured at 10, 20, or 30–35 m (but not 0 m) out of the total released (mean \pm 1 SE averaged across runways and batches). The movement rate (m day⁻¹) is the average for 294 individuals tracked past 10 m.

Microclimate and microhabitat features

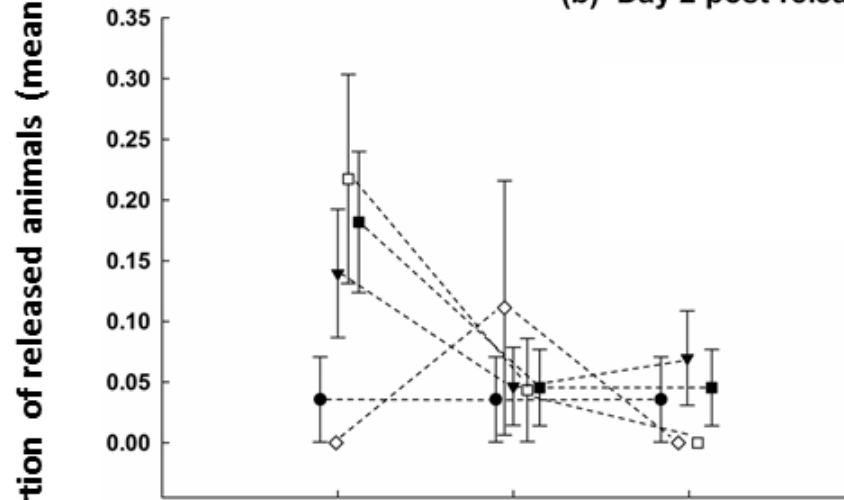
We observed moderate differences in microclimate among treatments (Table 1.2). Compared to the mature forest stands studied by Popescu & Hunter (2011), our ground-level maximum daily temperatures were, on average, 10.2–12.6 °C higher (2008–09, Table 1.2). The highest ground temperature was 42.3°C, recorded in the cornfield (13:00 h on 9 July 2010). The clearcut, hayfield, and moderate-cover lawn treatments were the driest (% relative humidity; Table 1.2). All treatments had 0% tree cover, except the moderate-cover lawn (45–85% canopy). In clearcuts, the herbaceous stratum had the

Figure 1.5. Timing of movements of juvenile *L. sylvaticus* experimentally released in five open-canopy treatments. The proportion of released individuals (y-axis) denotes the number moving through each station (averaged across runways and batches) relative to the total number of tracks recorded per runway (mean \pm 1 SE). The first three days post-release accounted for the majority of movement, with the exception of hayfield (note scale-bar difference for days 1 vs. 2 and 3). Because some individuals remained in the runways from earlier releases it is possible for the numbers at distant stations to exceed those at close stations (e.g., compare 10 m and 20 m in open lawn in panel c).

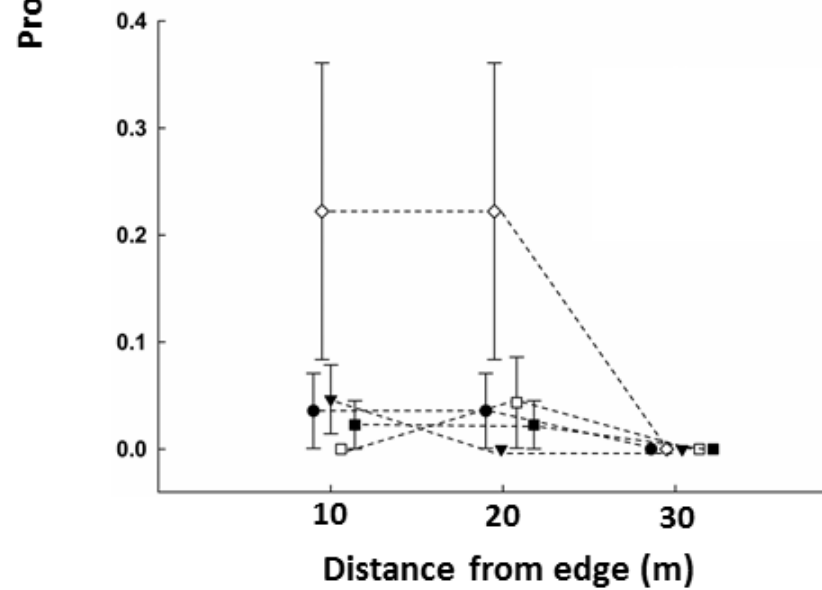
(a) Day 1 post-release juvenile *Lithobates sylvaticus*



(b) Day 2 post-release



(c) Day 3 post-release



greatest coverage (55.0%) and shrub cover was 11%. In the cornfield, the average inter-row distance was 1.1 m; average crop height grew from 1.6 to 2.8 m (16–29 July 2010). The hayfield had a tall, dense sward of grasses and legumes, with average stem height of 0.87 m (negligible differences between sampling dates) and density of 3280 stems m⁻². The lawns had high stem-densities (10,760 in moderate-cover; 12,880 in open lawn) but were much shorter: the open lawn grass grew from 10.7 to 17.4 cm between 16–29 July 2010 while the moderate-cover lawn was lower (8.6 and 11.4 cm on 16 and 22 July 2010, respectively; Table 1.2).

Discussion

In contrast to the traditional habitat-matrix paradigm, in which “habitat” is classified as hospitable and “matrix” as uniformly hostile (Hudgens et al., 2012), it is now recognized that species may perceive landscapes in complex ways, for example, by using resources from different land-cover types during dispersal. We tested the movements of juvenile *L. sylvaticus* in open-cover habitat types to evaluate how vegetation type affects permeability during dispersal, a critical stage for population connectivity. Few empirical studies have measured the effects of open cover on amphibian ranging and most of these have compared the permeability of forest to one type (e.g., old fields: Rothermel and Semlitsch 2002; grasslands: Rittenhouse and Semlitsch, 2006; clearcuts: Popescu and Hunter, 2011). In agroecosystems, crop-specific dispersal was compared for *Ambystoma tigrinum* (Cosentino et al., 2011) and *Rana temporaria* (Vos et al., 2007). This study is among the first to measure relative permeabilities across a broad spectrum of land-uses that generate open cover, with our

Table 1.2. Mean daily maximum temperature (°C) and relative humidity (%) of five open-canopy cover types (treatments) during experimental amphibian releases. Microclimate data are compiled for dates inclusive of frog movement through experimental runways (8 July–7 August 2010), and were recorded at ground- and refugia-levels in each runway.

Treatment	Mean daily maximum temperature (°C)			Relative humidity (%)
	Ground level	Refugia	Air	Ground level
2010				
Forest clearcut	33.5	27.3	34.9	60.0 ± 3.2
Hayfield	29.7	25.4	32.8	58.8 ± 3.3
Row crop (feed corn)	31.6	26.3	31.9	69.6 ± 3.5
Lawn (0% cover)	33.2	...	32.8	75.3 ± 3.6
Lawn (moderate, ~45–85% cover)	31.1	...	32.5	60.2 ± 3.6
2008 Reference				
Forest clearcut	31.6	23.4	...	62.9 ± 6.3
Mature forest	23.0	18.7	...	78.7 ± 4.5
2009 Reference				
Forest clearcut	26.3	22.1	...	86.3 ± 1.9
Mature forest	20.9	17.0	...	96.8 ± 1.0

Notes: Ellipses denote no data collected for: (1) refugia-level mean daily maximum temperature in 2010 (due to lack of micro-cover in lawn treatments); and (2) air temperature in the 2009–09 forest chronosequence stands (see Popescu & Hunter 2011). Relative humidity (%) was recorded at ground-level only (mean ± SE).

index (Appendix B) suggesting that permeability was lowest in row crops, increased in hayfields, clearcuts, and open lawns, and was highest in moderate-cover lawn. This pattern indicates that these are differential ecological filters to movements, and thus it is overly simplistic to assume dispersal success is singularly low across all open-cover types.

Habitat structure and locomotion

Our results suggest that the hayfield and forest clearcut may constitute physical filters to movement (i.e., locomotion constrained by dense ground vegetation), while the openness of the lawn and cornfield may have allowed faster movement. Although we predicted that open treatments would afford increased velocities for juvenile frogs, we did not anticipate the observed negative relationship between movement rate and an individual's willingness to enter a given treatment (Figure 1.4). Taken together, this suggests that simplified vegetation structure represented low impedance for locomotion, but that other factors (such as perceived predation or desiccation risk) may also shape entry decisions at the forest edge. In not one case did we observe a juvenile reach the 35-m mark during a single-night foray in the hayfield or clearcut. Moreover, velocities in the hayfield suggest that individuals may persist in this cover-type up to three days, post-release; this is a prolonged residency that we predicted for dense vegetation, although this result was rarely observed in other treatments (Figure 1.5c). Conversely, frogs in the cornfield and lawn exhibited more movement, evidenced by: (1) higher overall recapture rates at 30–35m, a result that was not predicted (Table 1.1); (2) greater number of single-night forays to the end of runways (Figure 1.5a, Table 1.1); and (3) greater average

velocity (Figures 1.4 and 1.5). Accordingly, previous studies have demonstrated that locomotor performances of amphibians depends on the nature of the surface component crossed (e.g. Eycott *et al.* 2012).

Potential influence of microclimate on permeability

Microclimate conditions play a role in the spatial ecology of amphibians (e.g., Dall’Antonia and Sinsch, 2001; Rittenhouse et al., 2008), but our results suggest limited links between temperature, humidity, and the physiology of frog performance. Our observed high temperatures and dry microclimates in the clearcut (Table 1.2) are consistent with low observed and predicted permeability in that treatment (Appendix A; Table 1.1). However, another low-permeability cover type, open lawn, had the highest relative humidity values and temperatures similar to other treatments, an unexpected result. Overall, most of our observed differences in microclimate were modest (Table 1.2), perhaps due to the relatively cool, moist climate of Maine, or perhaps due to the scale of our measurements (three per runway, one each for ground, air, and refugia). This contrasts with a number of studies suggesting that microclimate is a primary influence driving amphibian movements (e.g., Rittenhouse et al., 2008).

Direct mortality in open-canopy matrix habitats

Both microclimate and predation risk may influence the frequency and causation of direct mortality for post-metamorphic frogs, and these factors shaped our predictions for juvenile movements. For example, we expected open-canopy cover to have high risks of desiccation mortality if individuals could not find cool, damp refuge during

afternoons; anecdotally, we observed 6 deaths by desiccation in open lawn and 11 in cornfield. In open lawn, our most open treatment, this issue was avoided, at least by some frogs, which were released in the evening and captured at 35-m the following morning. As predicted, this never occurred in our least permeable and coolest treatment (hayfield: Table 1.2). We speculate that hayfield frogs could not travel through 35 m of thick vegetation in one night but that this treatment offered diurnal refugia for short-term persistence (Figures 1.4 and 1.5c). Predation is also likely to be higher in open cover than in forests (Barbasch and Benard, 2011; Lillywhite and Brischoux, 2012). We did not measure predator abundance, but anecdotally, we detected numerous *Thamnophis sirtalis* (garter snakes) in the hayfield, clearcut, and cornfield sites and we observed diurnal and nocturnal raptors (e.g., *Strix varia*, *Buteo jamaicensis*) near our agricultural treatments. If predation risk influences dispersal success, the occurrence of *T. sirtalis* in the clearcut and hayfield would align with their low permeability (Figures 1.1 and 1.4).

Single factors do not explain juvenile movements

We predicted that animals will respond to the interactive effects of vegetative cover, microclimate, presence of predators, and other factors such as landscape configuration during dispersal; thus, we would be unlikely to explain juvenile movements based on single factors. For example, the hayfield and open lawn represented the strongest filters to movement (Figure 1.2), yet these treatments had the greatest difference in relative humidity (58.83% and 75.30%, respectively) and understory vegetation, and the second-greatest difference in maximum daily ground temperatures (29.7° and 39.2°) among cover types (Table 1.2). Thus, there may be a conflicting role of the hayfield as a

filter and conduit to dispersal, since it may afford more cover, but at the cost of: (1) increased desiccation risk (i.e., low humidity, due to increased water-use efficiency of hay-crop species); and (2) greater impediments to locomotion (Figure 1.4). We posit that frogs were responding to an interplay of ecological pressures that reach beyond the factors discussed above to include density-dependent effects (Patrick et al., 2008), food availability (Niecieza, 2000), stress hormones (Janin et al., 2012), agrochemical or pollutants (Rohr et al., 2013), floral composition (Prevedello and Vieria, 2010), or range of perception (Vos et al., 2007).

The Evacuation Hypothesis and the fate of non-detected juveniles

Our data suggest that individuals may enter open cover during ranging, assess habitat quality, and subsequently change their decision. This is consistent with the “evacuation hypothesis” following clearcutting (Semlitsch et al., 2008), as well as our prediction that a greater proportion of animals would return to the forest edge when released in our most open treatments (i.e., lawns, cornfields; Figure 1.3). However, relatively high recapture rates at 35 m in the hayfield (29%), moderate-cover lawn (24%), and clearcut (20%) also suggest that individuals can travel an entire runway, once they made the decision to travel past 10 and 20 m. Furthermore, some of the longest single-distance movements (i.e., 35 m per night) occurred during dry ambient conditions. This indicates that juveniles may depart and move quickly through open treatments, once a direction is selected, corroborating results in clearcuts (*see* Table 1 in Popescu and Hunter, 2011). Lower recapture and track rates in the hayfield and clearcut indicated that they probably served as sources of refuge or mortality, a result that aligns with

predictions (Table 1.1, Figure 1.2). In our experiment, we cannot distinguish the fate of missing frogs with respect to mortality, trespass, and settling in the runway; or assess realized connectivity (i.e., survival to reproduction).

Future studies and management implications

To fully understand dispersal in heterogeneous, complex landscapes, we need long-term studies of individual ranging behavior in different cover types, both those typically deemed suitable habitat, as well as those that might facilitate dispersal but not be used during other life stages. Our study only provides a one-season window into the processes driving movements in human-altered landscapes. Our runway “self-tracking” design provide a minimally invasive way to record fine-scale ranging behavior, but a more complete understanding of the effects of open cover on dispersal requires long-term monitoring of individual fitness and behavior using direct tracking, although this remains a challenge for small-bodied organisms. We also need to assess how land management practices such as crop-rotation, thinning, harvest, mowing, pesticide application, or frequency of human disturbance or entry can be best designed (and situated within larger landscapes and across time) to facilitate dispersal. Disturbance intervals range from weeks in lawns to decades in clearcuts, and some disturbances happen during dispersal periods and some only in other seasons.

We have demonstrated that open-canopy cover types may differ as ecological filters to juvenile movements and these distinctions may inform land-use planning; for example, how the composition and configuration of these cover types should be integrated with forest distribution to reduce the “effective” isolation of (and not just

Euclidean distance between) preferred habitats. These distinctions are also important because many landscape population dynamics analyses use expert-based permeability values that are a one-size-fits-all measure for open cover (Kupfer et al., 2006; Yackulic et al., 2011; Hudgens et al., 2012). Our study provides a repeatable assessment of permeability at the scale of individual cover types and a quantitative permeability index, which can be used to parameterize models for amphibians, although we urge caution in the widespread application of this numeric index to other study species or regions (*see* Appendix B). Future research could use our understanding of the mechanistic aspects of permeability to explore movement through assemblages of different cover types (“landscape heterogeneity” scale), once technological capacity permits direct tracking of individuals over long distances. Thus, we also need field-based, direct measures of the mechanisms that influence ranging behavior and dispersal success in heterogeneous settings, in order to predict and effectively maintain functional connectivity in fragmented landscapes.

CHAPTER 2

HEAVY PARTIAL HARVESTS AND THE INITIAL MOVEMENTS

OF A DISPERSING FOREST AMPHIBIAN IN THE

ACADIAN FOREST OF MAINE, USA

Abstract

Maintaining amphibian populations in managed forests requires a balance between timber extraction and preserving functional connectivity for animals that need to transit multiple vegetation types to satisfy habitat requirements, particularly in regions where extensive harvesting may increase forest fragmentation. For pool-breeding amphibians, population viability is maintained through juvenile dispersal; thus, quantifying the willingness of dispersers to enter harvested areas across high-contrast edges adjacent to unlogged forest remains a fundamental need. We tested the initial dispersal orientation of juvenile wood frogs (*Lithobates sylvaticus*) at silvicultural edges in partial harvests (31-60% retention standwide) in the Acadian forest region (Maine, USA) to evaluate if dispersers would enter harvested areas. We conducted experimental releases of juveniles ($n = 621$) in nine 10m diameter arena enclosures spanning silvicultural edges between control forest and partial harvests in order to document their selection of initial habitat. Uncut control forest (~ 70-75% closed canopy) was contrasted to one of three possible conditions in the partially-harvested stand: (1) harvester trails (0% retention) running parallel to the edge of uncut forest; (2) harvester trails running perpendicular to the edge; or (3) residual strips of partially-cut matrix forest (~30% retention) between trails. Overall, we observed a slightly greater, statistically

insignificant, percentage of individuals enter control (54.8%) relative to combined treatments (45.2%; p -value = 0.113). Perpendicular harvester trails may represent a partial filter to movements as juveniles showed near significant selection of control forest within that treatment (59.8% versus 40.2%; p -value = 0.068). Lower recapture percentages in treatments adjacent to residual strips of partially-cut forest relative to parallel harvester trails (35.2% versus 53.1%; p -value = 0.013) also suggest that residual strips (but not trail) treatments may afford cover. From a management standpoint, juveniles may occupy partial harvests (>30% canopy retention) at rates similar to intact forest during dispersal, but the spatial configuration of trails and residual strips may affect amphibian population connectivity.

Introduction

Integrating timber management goals with biodiversity conservation often involves linking management of unlogged areas with appropriate forest practices on harvested areas, especially for relatively mobile animals that navigate multiple vegetation types to meet habitat needs (Hunter and Schmiegelow, 2011; Driscoll et al., 2013). For amphibians in managed forest landscapes, quantifying the willingness of natal dispersers to enter harvested areas across high-contrast (“hard”) edges adjacent to unlogged forest remains a critical challenge to predicting their population responses to forest harvesting. This issue gains additional traction as silvicultural methods shift away from intensive clearcutting toward partial harvesting, since the cumulative effects of multiple stand entries implemented over large areas may only increase the effects of habitat fragmentation, and impacts on amphibian populations remain unknown (e.g., Vanderwel

et al., 2009; Homyack and Haas, 2013). Successful dispersal often depends on the characteristics of the matrix that intervenes between suitable habitats (Kuefler et al., 2010; Burgess et al., 2012); thus, quantifying the habitat selection of individuals as they encounter logging-induced edges could have important implications for maintaining functional connectivity as harvest practices trend away from even-aged management.

In recent decades, understanding the effects of forest management on amphibian populations has been of particular concern due to their demonstrated sensitivity to habitat loss or fragmentation (deMaynadier and Hunter, 1995), biphasic lifestyles linking terrestrial and aquatic systems (Cushman, 2006), and potential keystone role in forest ecosystems as abundant apex predators in detrital food webs (Walton, 2005). Many studies have documented the long-term negative impacts of complete canopy removal (i.e., clearcutting) on amphibian distribution and abundance (e.g., Karraker and Welsh, 2006; Popescu et al., 2012a, etc.). Similarly, high-contrast edges between recently cut and mature forests have low permeability to movements (Stamps et al., 1987; Popescu and Hunter, 2011; Cline and Hunter, 2014), likely due to higher levels of sunlight, wind speeds, and greater variation in humidity and temperature found at the edge relative to the forest interior (Harper et al., 2005). Yet, there remains a critical need to assess amphibian movement across forested landscapes that may be fragmented by logging because long-term population viability depends on juvenile dispersal, or the unidirectional movement of some juveniles from the pool where they hatched to a new breeding pool (Semlitsch, 2008; Walston and Mullin, 2008). In contrast to conventional assumptions of patch-matrix models that oversimplify the non-forested matrix as inhospitable, recent evidence suggests that frogs may transit various (including open-

cover) vegetation types during dispersal, even if they are unsuitable for settling (Cline and Hunter, 2014). Therefore, behavioral studies are necessary to elucidate the factors influencing juvenile movements in forests fragmented by logging – and specifically, to quantify the willingness of dispersers to enter and transit various harvested and non-harvested vegetation types within the matrix (Revilla et al., 2004; Van Buskirk 2012).

The need to assess amphibian dispersal behavior in forestry settings is particularly pressing in northeastern North America, where harvesting practices have shifted from a heavy reliance on intensive clearcutting in distinct patches to extensive partial harvesting. Typically, such partial harvests are implemented in herring-bone patterns of parallel harvester machine trails (3-4 m wide) spaced 15-20 m apart; often 40-60% of the matrix stand between the trails is also removed (Sader et al., 2003; Bataineh et al., 2013; Figure 2.1). Partial harvesting is currently the predominant form of timber extraction in Maine, accounting for 176,579 of the total 186,703 harvested hectares during 2012 (Maine Forest Service 2013). This trend has been attributed to changes in forest policy, market conditions, equipment technology, silvicultural knowledge, and land ownership (Sader et al., 2003; Homyack and Haas, 2013). Multiple harvesting entries using a diversity of cut-to-length and forwarding equipment results in variable stocking, stand structure, and fragmentation patterns. Thus, the term “partial harvest” is an umbrella term, broadly described as any harvest that removes a portion of the stand, often implemented in multiple entries during a single rotation (Brissette, 1996).

However defined, there is a limited understanding of how heavy partial harvesting implemented in a herringbone pattern affects regeneration, future stand structure, or landscape-level forest composition. Given the increasingly common use of this harvest

practice in northeastern forests, the dearth of information further hinders our ability to devise silvicultural prescriptions, project future wood supplies, and assess impacts on biodiversity (Driscoll et al., 2013). For example, in a review of wildlife responses to partial harvesting (*sensu lato*), researchers found that 38 of 65 vertebrate species associated with mature or old boreal forest decreased in abundance following high-intensity harvesting (30% retention; Vanderwel et al., 2009; also *see* Rosenvald and Lõhmus, 2008), a result corroborated by other studies that document a negative relationship between harvest intensity and amphibian habitat use (e.g., Harpole and Haas, 1999; Homyack and Haas, 2009). However, few studies provide a mechanistic or modeling basis for linking the patterns of structural change to faunal response (e.g., Vanderwel et al., 2011), and thus there is a need to investigate species responses through experimental studies of behavior. Throughout the Acadian region, partial harvesting is increasing fine-scale spatial heterogeneity (as depicted in Figure 2.1) at widely varying harvesting intensities, which raises concerns about the effects of this form of forest management on amphibian dispersal behavior and consequent population response.

Study species

We studied the wood frog (*Lithobates sylvaticus*) due to its widespread distribution in North America and its dependence on closed-canopy forest. This species has demonstrated high sensitivity to forest removal (Cushman, 2006) and avoids proximity to forest edges (deMaynadier and Hunter, 1998; Semlitsch et al., 2008). Following emergence from natal pools, juveniles inhabit moist terrestrial landscapes, foraging on invertebrates and hibernating within refugia (e.g., burrows, tree root

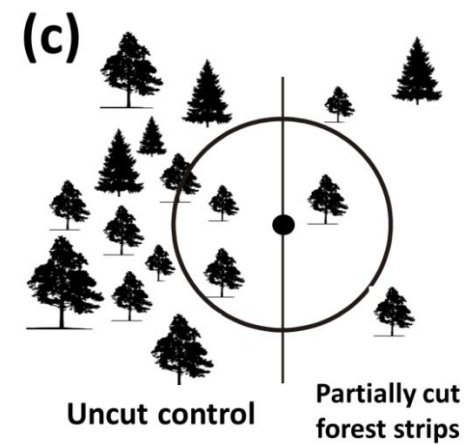
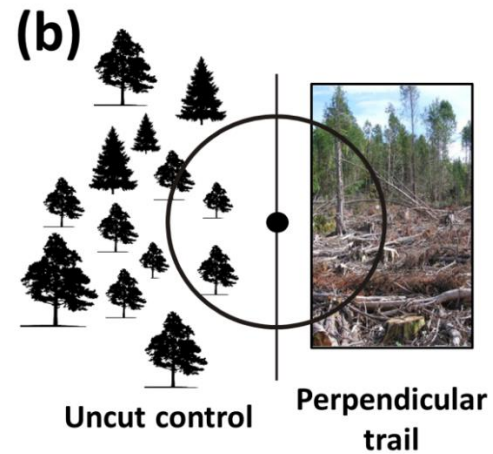
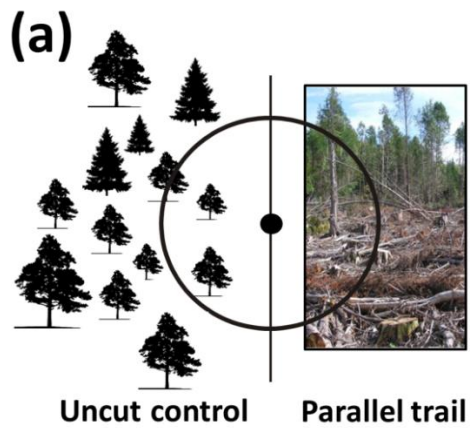
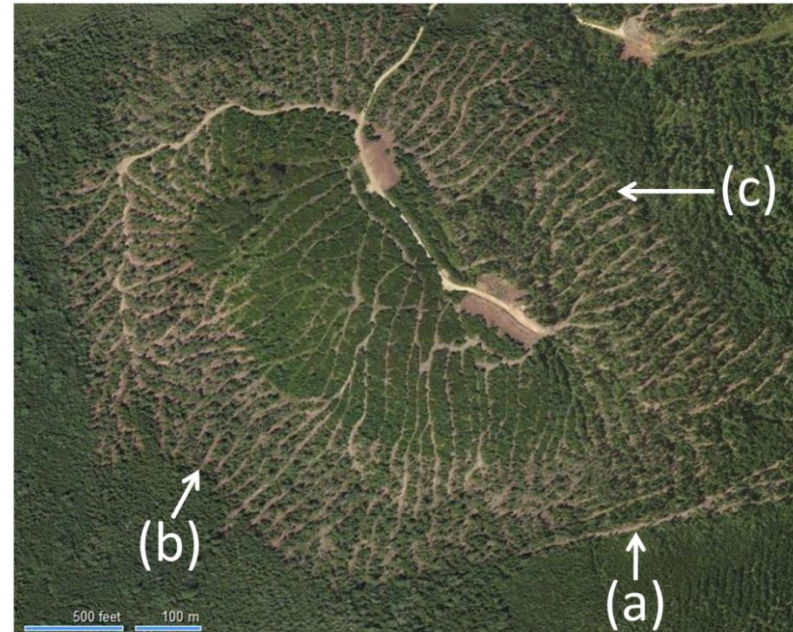
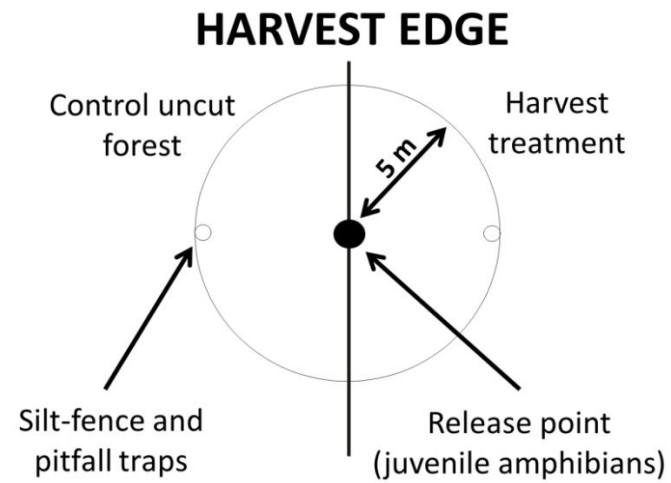
channels, leaf litter, and coarse woody material). Dispersal success (i.e., juveniles surviving to breed in new sites) is estimated at 18–20% (Berven and Grudzien, 1990). Dispersal distances have been recorded at > 1000 m (females: 1140 ± 324 m; males: 1276 ± 435 m), with a maximum of 2530 m (Semlitsch and Bodie, 2003). Post-breeding movements of adults have been estimated at 102–340 m (Baldwin et al., 2006), and > 300 m (Vasconcelos and Calhoun, 2004). Thus, the scale of overland movements may make this species particularly vulnerable to loss of connectivity during the juvenile phase.

Study goal and hypotheses

In this experiment, our goal was to document the short-term behavioral response of juvenile wood frogs in their selection of initial dispersal habitat. Uncut control forest was contrasted to one of three possible conditions in the partially-harvested stand: (1) harvester trails running parallel to the edge of the uncut forest; (2) harvester trails running perpendicular to the edge; or (3) residual strips of partially-cut matrix forest between trails (Figure 2.1).

Given that partial harvesting: (1) reduces canopy cover overall; and (2) eliminates canopy cover completely in the harvester trails (cumulatively comprising >20% of the managed forest stand), our guiding hypothesis was that juveniles would prefer unharvested controls over partially-cut stands. We further hypothesized that the duration of responses would be more protracted in the control forest, if some frogs were able to occupy suitable microhabitats in the experimental area. We also speculated that harvester trail orientation might influence responses. Specifically, we conjectured that parallel trails would be more permeable to movements than perpendicular trails.

Figure 2.1. Experimental design for evaluating the initial dispersal orientation of juvenile wood frogs (*Lithobates sylvaticus*) in 2011 along three types of linear edges between our partial harvest treatments and intact forest (closed-canopy mixed-wood stands directly adjacent to heavy partial harvests). Silvicultural edge treatments included tracts of uncut control forest located: (a) parallel to harvester trail (trail within cut; 100% canopy removal); (b) perpendicular to harvester trail (trail within cut; 100% canopy removal); and (c) adjacent to residual strips of partially-cut forest (off-trail). Each experimental arena (two replicates of each edge treatment, for a total of n= 9 arenas in two study landscapes) consisted of a 5-m radius (10-m diameter) circular silt-fence enclosure (40-50 cm height), extending 10-15 cm in the ground. Two pitfall traps (indicated by circles above) were buried on the fence interior of each arena, located in opposite cardinal directions and extending into each edge treatment to test initial frog orientation following experimental release (mark-recapture).



Materials and Methods

Study sites

Our experiment was conducted in Penobscot County, Maine, USA on harvests prescribed by American Forest Management, Inc. (AFM). We are confident that these were representative of current practices in the region, in part because AFM's Northeast Region currently manages greater than 400,000 hectares in Maine and New Hampshire (T. Massey; *pers. comm.*; <www.afmcorporate.com>). We used two study sites in Titcomb Pond and Great Pond Townships, Maine (44.94°N, 68.43°W and 44.99°N, 68.31°W, respectively) that had similar prescriptions, but edges that were oriented in different cardinal directions relative to trails. Multiple harvesting entries occurred on our sites; intensive even-aged harvesting was conducted in the late 1980s, but more recent harvests were broadly categorized as 2nd or 3rd stage shelterwoods with harvesting traffic concentrated in parallel strips (Figure 2.1). The most recent timber removal occurred in 2008 or 2009, with final shelterwood removal pending. All harvests were performed using whole-tree removal (Timbco 425 track harvester and grapple skidder) with de-limbing off-site; trails were devoid of canopy and diminished in cover objects that might serve as refuge for amphibians.

Our study region is characterized by a humid continental climate (Köppen classification *Dfb*; Peel et al., 2007), with warm-hot, humid summers and cold-severely cold winters, and is part of the Acadian Forest region (Seymour, 1995), a transitional zone between the temperate forest and boreal forests. Partial disturbances from insect, wind, and natural senescence and small-scale gap dynamics likely characterized the presettlement natural disturbance regime (Seymour et al., 2002; Fraver et al., 2009).

However, extensive forest management has generated a mosaic of mixed-wood stands of various age classes (e.g., Olson and Wagner, 2010; Arseneault et al., 2011).

Our sites comprised a mixture of northern conifers and tolerant hardwoods: red spruce (*Picea rubens*), balsam fir (*Abies balsamea*), eastern hemlock (*Tsuga canadensis*), eastern white pine (*Pinus strobus*), northern white cedar (*Thuja occidentalis*), red maple (*Acer rubrum*), bigtooth aspen (*Populus grandidentata*), paper birch (*Betula papyrifera*) and American beech (*Fagus grandifolia*). The stand composition in partially-cut forest indicated a shift toward hardwood dominance (30-70% basal area). The prescription goal was to maintain 80% forested conditions, with 20% occupied in trails and a stand-wide nominal goal of 31-60% crown closure (with 0% closure in the center of harvester trails this would mean 39-75% in the residual strips). We documented 27.4 – 30.4% average canopy cover across residual strips, suggesting a stand-wide closure of about 23%. The width of skid trails ranged 4.9 – 5.5 m, depending on size of equipment and trees. The distance between harvester trails (center to center, not edge to edge) was 22.8 – 27.4 m. Our closest experimental arenas were 124 m apart, and the farthest 12.7 km apart.

Experimental design and arenas

We constructed nine experimental arrays at the edge of intact forest and partially-harvested stands representing our three treatments (i.e., closed-canopy control forest located at an edge: adjacent to residual strips of partially-cut forest between trails, perpendicular to harvester trail, or parallel to harvester trail; Figure. 2.1). We built 10m diameter arenas (completely enclosed) using partially opaque polyethylene silt-fence 40-50 cm in height plus 10-15 cm buried in the ground. We buried two pitfall traps along the

inner perimeter of fence walls, one in the middle of the control forest portion of the fence, and another directly opposite. Pitfalls consisted of two 10-cm aluminum coffee cans taped together and buried 24 cm in the ground, with a 10-cm deep funnel extending into buckets. We checked traps daily between sunrise and 10:30 AM and assigned each frog to control forest or partial-harvest treatment based on location of capture (Figure 2.1).

Juvenile amphibian rearing and release

Prior to the experiment, we collected *L. sylvaticus* egg masses from the University of Maine's Dwight B. Demeritt Experimental Forest, Maine, USA (44.92°N, 68.67°W) during the spring egg-laying season (April – May 2011) and raised these in plastic wading pools at a forested site until hatching using methods described in chapter 1 and published in Cline and Hunter (2014).

Prior to each release, we measured (snout-vent length), marked (single different toe clip per batch), and randomly assigned frogs to one of our two study sites, three treatments, and nine arenas. We released 7–18 frogs per batch; frogs were placed at the forest edge and in the arena center 1–2 h after sunset. We released 621 *L. sylvaticus* across five batches (6, 12, 15, 18, and 26 July 2011). We released subsequent batches only after recapture rates were > 40% of the total number released in prior batch. By waiting 3–8 days between batches, most frogs from prior releases had been recaptured (minimizing density-dependent effects). Arenas were checked daily 06:30–11:00 h (7 Jul – 6 Aug 2011); frogs were returned to forest near their pools of natal origin.

Microclimate and habitat sampling

We characterized microclimate, microhabitat, and stand-scale vegetation within arenas and adjacent control and partially-cut forests. We recorded hourly temperatures (°C) and relative humidity (%) using 36 iButton hygrochron data loggers for the duration of the experiment (Maxim, Inc., Dallas Texas, USA). Temperatures were measured at the center of each arena at: (1) ground-level; (2) under refugia (i.e., 5–8 cm below coarse woody material or slash); and (3) 120 cm above ground in shade; we also measured ground-level relative humidity (4). In addition, we sampled hourly temperature in control forest and partial-harvested treatments 15 m from the edge.

We characterized vegetation and microhabitat in terms of ground cover, canopy closure, vegetation height, dominant species composition, leaf litter depth, and soil moisture. Sampling occurred in 54 3 x 3 m (9 m²) plots positioned (1) within each arena (2 plots per arena; 1 in control, and 1 in partial-harvest treatment semi-circle); and (2) outside of each arena, 10 m into each control or treatment (4 plots per arena). We measured percent vegetation cover in four height classes (0-0.5, 0.5-1, 1-2, and > 2 m), and dominant composition at the tree, shrub, and herb level. We estimated percent canopy cover using a densitometer (Moosehorn CoverScopes, Medford, OR, USA). We estimated ground cover as the percentage of 3 x 3 m plots classified as: leaf litter, moss / lichen, herbaceous, slash, bare soil, and rocks. We collected leaf litter depths and soil moisture (FieldScout TDR 100 soil moisture meter; Spectrum Technologies, Aurora, IL, USA) at 3 randomly-determined locations per plot.

Analytical approach

To assess the initial dispersal orientation of each frog relative to the forest edge and recapture outcomes, our dependent variable was the proportion of frogs that was recaptured in the control versus treatments out of the total released per treatment, arena, and batch. We employed pairwise tests for proportions and chi-square tests to estimate differences in proportions of recaptures at the individual and batch levels.

We also evaluated potential differences in movement timing (1-25 days following release). For each recaptured frog, we calculated the number of days that had passed between the date of initial release and final recapture and evaluated differences using a non-parametric (chi-squared) Kruskal-Wallis test for proportions (R package [coin]; Hothorn *et al.* 2008). We examined the goodness of fit of our observed movement timing data (i.e., the number of individuals recaptures on days 1-25 post-release, pooled by treatment) relative to predicted values using a nonlinear mixed-effects model, allowing for nested random effects and assuming a non-linear exponential decay function (R package [NLME]; Lindstrom and Bates, 1990; Pinheiro and Bates, 2000).

We assessed potential differences in the size of metamorphs (SVL) released among treatments and arenas using a one-way analysis of variance (ANOVA) and Tukey's honestly significant difference (HSD) single-step test for multiple comparisons. Statistical tests were deemed significant at $P < 0.05$ and marginally significant at $P < 0.07$. All statistical tests were conducted in Program R Version 3.0.2 (R Development Core Team, 2013).

Results

Our experimental design generated three simple metrics to quantify the initial dispersal orientation of juvenile *L. sylvaticus* released at partially-harvested forest edges: 1) the initial choice of movement direction for individuals recaptured; 2) the percentage of recaptures; and 3) movement timing and latency (described below). The average size (snout-to-vent length; SVL) of juveniles was 15.4 ± 0.1 mm (Figure 2.2), with no significant differences among batches 2-5 (i.e., 12, 15, 18, and 26 July 2011). However, batch one individuals (6 July) were significantly smaller (13.9 ± 0.1 mm; $F_{1,243} = 4.27$, p -value < 0.001 ; ANOVA; Tukey's HSD; Figure 2.2).

Willingness to enter harvests: Initial dispersal orientation and proportion of recaptures

Overall, we observed a greater proportion of individuals enter control forest (54.8%) than partial harvests (45.2%; Figure 2.3; based on the distribution of 270 recaptured individuals out of 621 released). However, a test for global significance (i.e., forest captures vs. treatment captures summed across sites, arenas, and batches) was not significant ($\chi^2_1 = 2.504$, p -value = 0.113). Analysis by individual treatment revealed a near-significant difference for the edges that were oriented perpendicular to harvester trails (captures = 52:35 for forest vs. treatment; $\chi^2_1 = 3.322$, p -value = 0.068; Figure 2.3), but none in arenas located adjacent to parallel harvester trails (57:53 for control forest and treatment, respectively; $\chi^2_1 = 0.146$, p -value = 0.703), or at the confluence with residual strips (39:34 for control vs. treatment; $\chi^2_1 = 0.343$, p -value = 0.558).

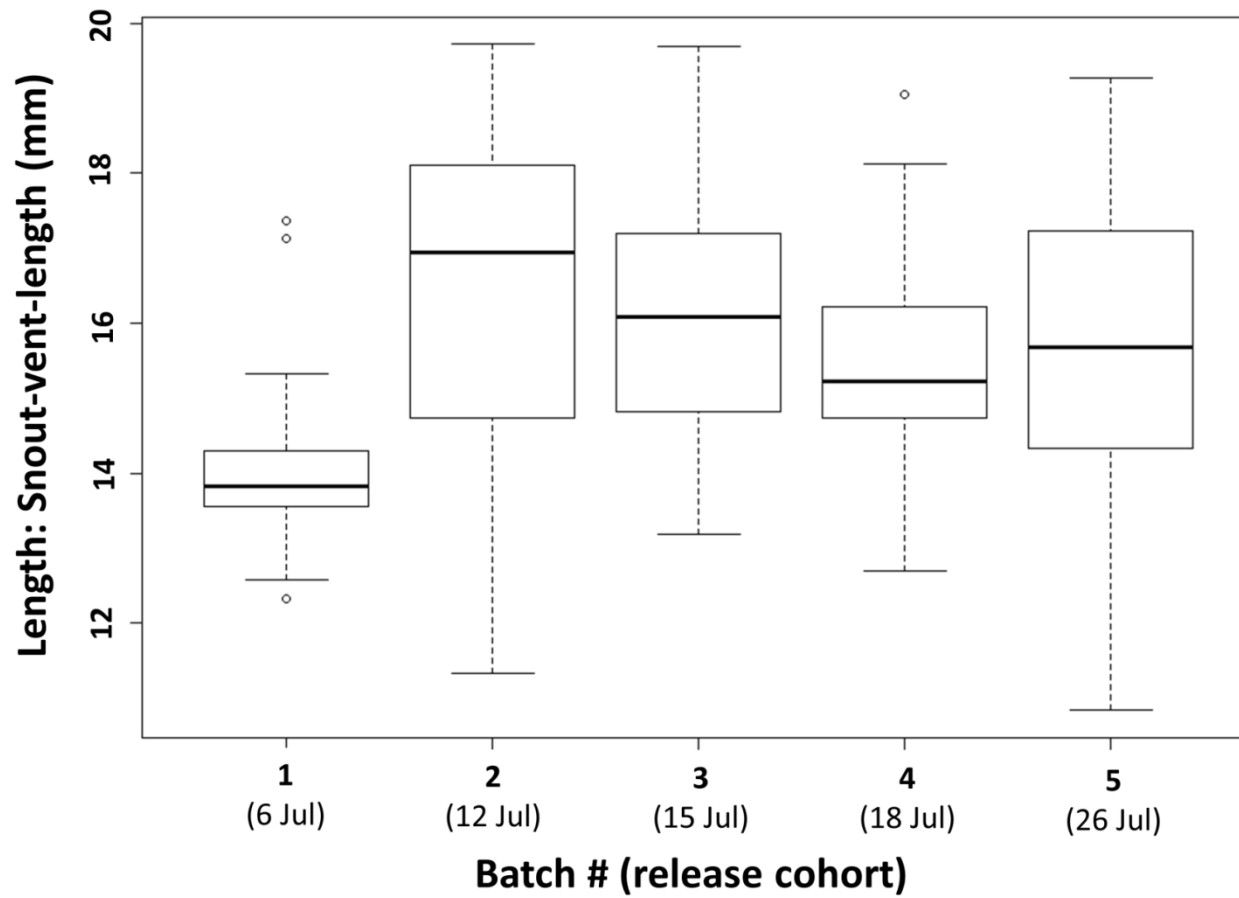


Figure 2.2. Lengths (snout-vent-length) of juvenile *L. sylvaticus* experimentally released along silvicultural edges in partial harvests during five batches in 2011 (6, 12, 15, 18, and 26 July). Only individuals released early in the juvenile emergence period (i.e., batch 1) were significantly different in size from the other batches ($F_{1,243} = 4.27$, p -value < 0.001 ; ANOVA; Tukey's HSD).

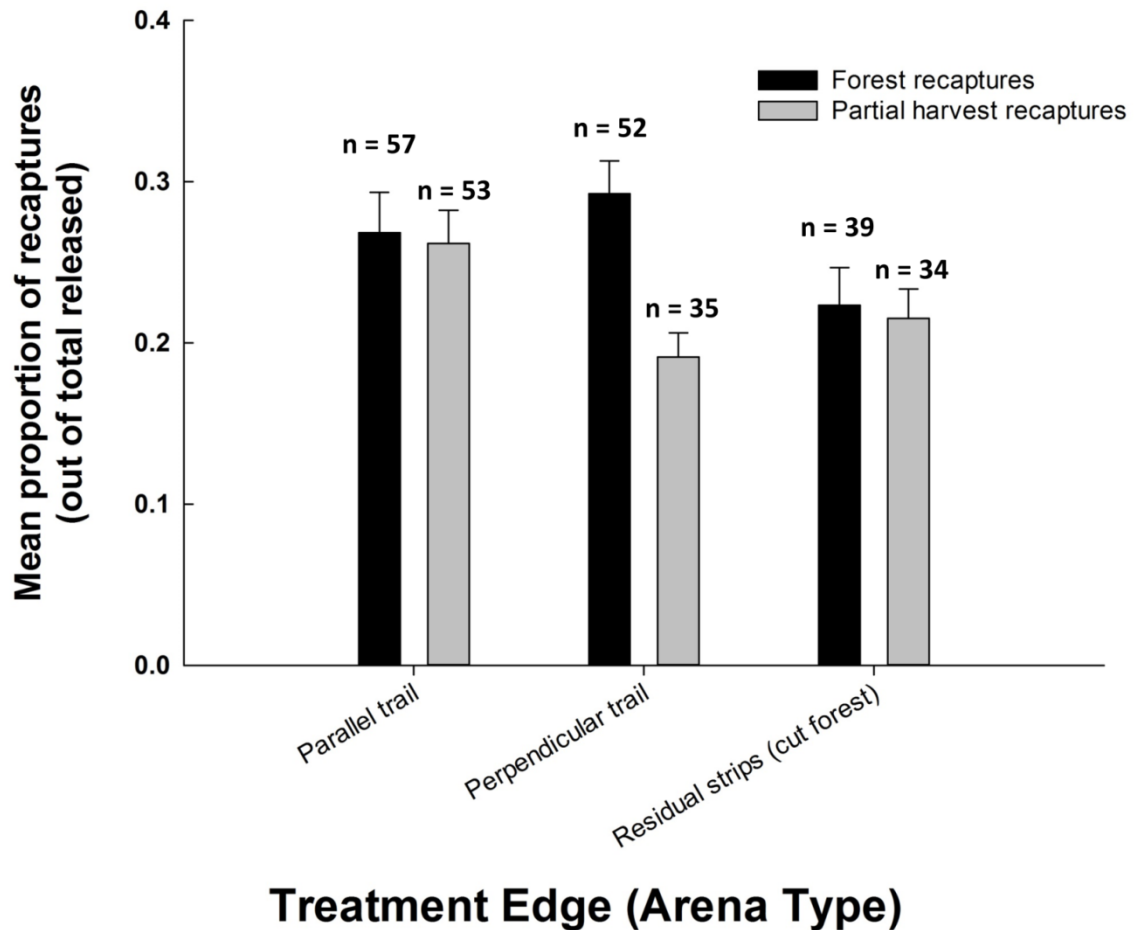


Figure 2.3. Observed proportions of juvenile *L. sylvaticus* recaptured in forest or partial harvest treatments, following experimental releases along three types of silvicultural edges between contiguous control forest and heavy partial-harvested stands in 2011 (mean \pm SE). Silvicultural edge treatments included tracts of uncut control forest located: (1) parallel to harvester trail (trail within cut; 100% canopy removal); (2) perpendicular to harvester trail (trail within cut; 100% canopy removal); and (3) adjacent to residual strips of partially-cut forest (without harvester traffic) within the harvested stand. Values on y-axis are observed proportions of released individuals recaptured in pitfall traps averaged across treatments ($n = 3$ arena types), individual arenas ($n = 9$ arenas), and experimental batches (constituting 621 individual frogs released during 5 batches between 7 Jul and 2 Aug 2011). Differences in the orientation of recaptured juvenile frogs approached significance in the edge treatment with perpendicular trail configuration (middle bars in above graph; $\chi^2 = 3.322$; p -value = 0.068).

Willingness to depart harvest edge: Percentage of frogs recaptured in experimental arenas

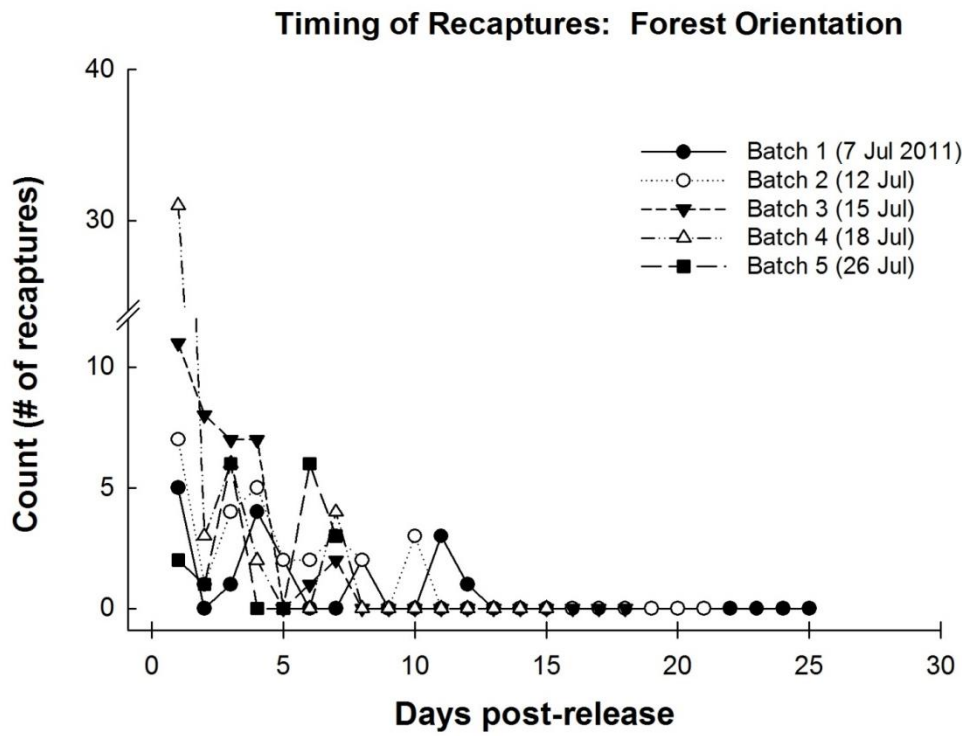
Across all treatments and arenas, the percentage of recaptures (out of total released) was 43.2% (270/621; Table 2.1). We observed the lowest proportion of recaptures in the control versus residual strip arenas (30.4 – 36.2%); in contrast, we observed the highest number of recaptures (and potentially lower frog settling rates) within arenas located at the edge of harvester trails (mean % recaptures = 42.0% for perpendicular trails and 53.2% for the parallel trails; $\chi^2_8 = 19.20$, p -value = 0.013; Table 2.1). Among batches, the percentage of recaptures was greater earlier in the emergence season (43.1 – 51.0% between 6-18 Jul versus 27.8% for those released on 26 Jul) although these differences were insignificant ($\chi^2_4 = 0.751$, p -value = 0.111).

Latency at the edge: Movement timing and potential short-term residency

Most movements (92.5%) occurred within the first 8-10 days following an experimental release and the timing of movement did not differ significantly between control forest and partial-harvest treatments (Figure 2.4; p -value = 0.693 for comparison of GLNS models). However, it is noteworthy that individuals could persist along the forest edge (presumably in a period of temporary settling or latency) for up to 25 days, post-release. It is also worth noting that treatment side captures occurred first (59.2% by day 2 vs 46.6% for control side; Figure 2.4) although the difference was not significant ($\chi^2_1 = 1.501$, p -value = 0.221).

Figure 2.4. Timing of movements of juvenile *L. sylvaticus* experimentally released in three treatments in enclosed arenas along silvicultural edges between control forest and partially-harvested stands. The number of recaptured individuals (y-axis) denotes the number recaptured in either the forested (panel a) or partially-harvested (panel b) semi-circle of each experimental arena out of the total released for that treatment and arena (mean \pm SE). Each line of the response designates one of five experimental release dates, or batches (constituting 621 individual frogs released during 5 batches on 6, 12, 15, 18, and 26 Jul 2011). The first 8-10 days accounted for the majority of movements as detected by recaptures (however, note the scale bar difference for the response variable between graphs). Individuals not recaptured by the conclusion of the experiment (2 Aug 2011) may have suffered direct mortality or settled in the arena.

(A)



(B)

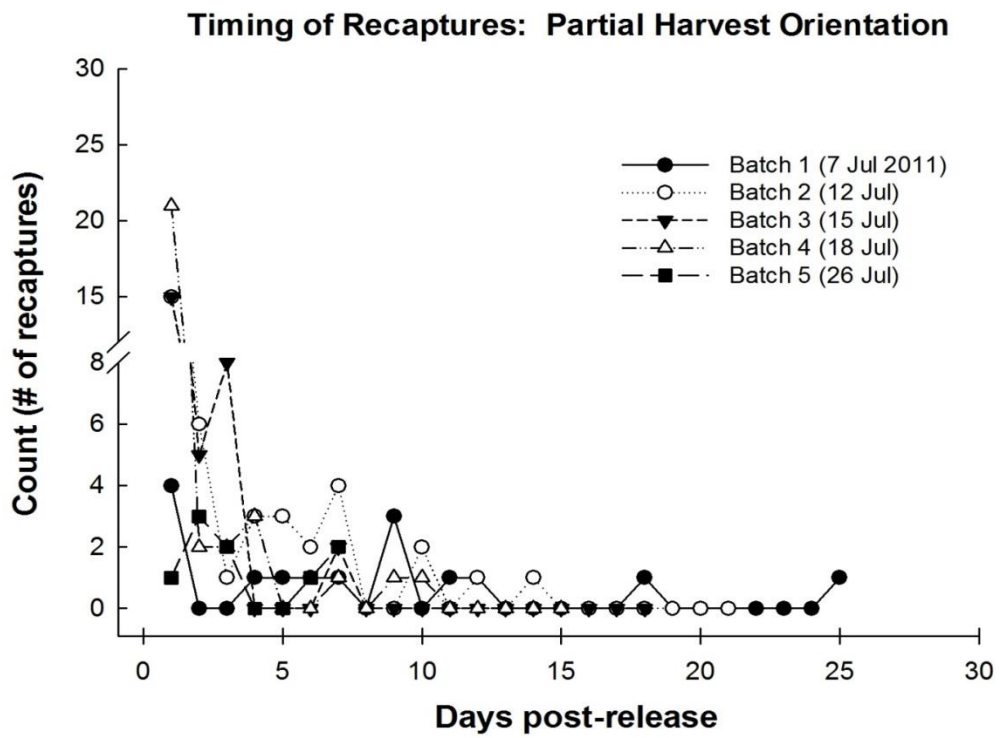


Table 2.1. Numbers of juvenile wood frogs (*L. sylvaticus*) recaptured in experimental arenas following releases in enclosed arenas located along three types of silvicultural edges between control forest (CF) and three partial-harvest treatments (parallel harvest trail; perpendicular harvest trail; residual strips of partially-cut forest between trails) in 2011. Harvest trails have complete overstory removal; residual strips are off-trail (~ 30% retention). Data are proportion of recaptures in either the forested or partially-harvested treatment out of the total released, further categorized by individual arena and batch.

Table 2.1.

Site	Treatment	Arena #	No. juveniles released	Individuals recaptured by site, treatment, and arena	
				No. juveniles recaptured	Proportion recaptures
Titcomb	CF - Parallel	1	69	46	0.667
	CF - Perpendicular	2	69	31	0.449
	CF - Residual strips (cut)	3	69	25	0.362
Great Pond	CF - Parallel 1	4	69	32	0.464
	CF - Parallel 2	5	69	32	0.464
	CF - Perpendicular 1	6	69	30	0.435
	CF - Perpendicular 2	7	69	26	0.377
	CF - Residual strips (cut)	8	69	27	0.391
	CF - Residual strips (cut)	9	69	21	0.304
Totals:		9	621	270	
Batch #	Release date		No. juveniles released	Individuals recaptured by batch (date of experimental release)	
				No. juveniles recaptured	Proportion recaptures
1	6-Jul-11		65	33	0.508
2	12-Jul-11		144	67	0.465
3	15-Jul-11		153	66	0.431
4	18-Jul-11		162	77	0.475
5	26-Jul-11		97	27	0.278
Totals:			621	270	
Mean recapture proportion:					0.432

The harvested and forested edge: Microclimate and microhabitat features

As expected, we observed a $> 10^{\circ}\text{C}$ difference in average daily maximum temperatures between control forest and partially-cut forest stands at points 10m from the forest edge (23.7°C vs. 33.9°C , respectively; Table 2.2). Within arenas, we observed the lowest daily maximum air, ground, and refugia temperatures in the residual strips between trails (31.8° , 33.9° , and 30.7° , respectively; Table 2.2), and the highest average daily maximum at ground level in arenas within the harvester trails (40.4° and 38.8° in parallel and perpendicular treatments, respectively). On average, treatment edges maintained similar levels of relative humidity at ground level (84.3% - 88.6%), although the mean daily minimum humidity values showcase the wide range of possible moisture levels (driest in the parallel trail treatments at 37.8%; Table 2.2).

By design, the control had high canopy cover, both within and outside of arenas (68% and 73%, respectively; Table 2.3). Tree canopy constituted moderate cover in the residual strip treatments (27% and 30% within and outside of arenas), which was below the prescribed target range (31-60% crown closure). In contrast, low vegetation layers (0.5 – 2 m) dominated harvester trails; herbaceous and shrub layers constituted 24 - 35% of cover, concordant with overstory removal (tree canopy cover: 19.6% and 6.4% within and outside of arenas, respectively; Table 2.3).

For ground cover, the leaf litter and moss categories together accounted for $> 70 - 89\%$ in control forest, while herbaceous vegetation and slash comprised high coverage in trails (31% and 21%, within arenas; 21% and 40% outside arenas; Table 2.3). Treatments in the residual strips had moderate leaf litter (45% and 28% within and outside arenas, respectively) and greatest slash coverage (20% and 14%). Soil moisture

Table 2.2. Mean daily maximum temperature ($^{\circ}\text{C}$) and relative humidity (%) of control forest and three partial-harvest treatments during experimental amphibian releases along silvicultural edges. Microclimate data are compiled for dates inclusive of frog movement within experimental arenas (7 July – 10 August 2011), and represent the mean values across all days and arenas. Temperature data were recorded at air-, ground- and refugia-levels in each arena and extending > 10 m into each adjacent edge (outside of arena). Relative humidity data were recorded at ground level in each arena.

Treatment	Mean daily maximum temperature ($^{\circ}\text{C}$)			Relative humidity (%)	
	Ground level	Refugia	Air	Mean daily (%)	Mean daily minimum (%)
Within arena					
At edge (control forest treatment)					
CF parallel trail	40.43 ± 1.51	34.83 ± 1.05	32.60 ± 1.09	85.03 ± 2.59	37.84 ± 5.28
CF perpendicular trail	38.79 ± 1.73	31.54 ± 0.79	34.19 ± 1.12	88.60 ± 4.71	59.21 ± 7.11
CF residual cut strips	33.93 ± 1.34	30.71 ± 0.81	31.77 ± 0.97	84.27 ± 2.35	47.48 ± 4.21
Outside arena					
Control forest	23.70 ± 0.41
Residual strips of cut forest	33.91 ± 1.23

Table 2.3. Habitat characteristics of control forest and three partial-harvest forestry treatments in central Maine during experimental amphibian releases along silvicultural edges (mean \pm SE) in 2011 (6 July – 10 August).

Treatment	Cover of vegetation layers (%)				Ground cover (%)						Leaf litter depth (cm)	Soil moisture (%)
	≤ 0.5 m	0.5 - 1 m	1-2 m	Tree canopy	Leaf litter	Moss / lichen	Herbaceous	Slash	Bare ground	Rocks		
Within arena												
Control forest	23.3 \pm 8.1	22.3 \pm 6.4	19.4 \pm 5.0	67.9 \pm 7.6	48.1 \pm 10.8	28.0 \pm 9.1	9.8 \pm 1.5	7.0 \pm 1.5	6.7 \pm 6.3	0.4 \pm 0.3	2.4 \pm 0.5	15.9 \pm 1.7
Residual cut forest	3.7 \pm 1.3	6.3 \pm 2.7	7.0 \pm 4.2	30.4 \pm 10.4	45.0 \pm 18.9	26.7 \pm 2.9	7.7 \pm 2.8	19.7 \pm 5.2	0.7 \pm 0.6	0.3 \pm 0.3	2.5 \pm 0.6	13.9 \pm 1.6
Harvester trail	32.5 \pm 7.7	24.2 \pm 7.9	12.8 \pm 4.0	19.6 \pm 7.9 ^a	22.2 \pm 6.9	14.5 \pm 6.0	30.5 \pm 7.2	21.2 \pm 6.7	9.2 \pm 4.4	0.8 \pm 0.7	1.4 \pm 0.3	20.8 \pm 3.2
Outside arena												
Control forest	10.8 \pm 2.9	17.7 \pm 5.0	21.9 \pm 5.4	72.9 \pm 4.6	45.1 \pm 7.9	43.6 \pm 7.8	6.2 \pm 0.9	4.3 \pm 1.0	0.3 \pm 0.2	0.6 \pm 0.6	2.1 \pm 0.3	23.2 \pm 3.3
Residual cut forest	6.8 \pm 1.9	5.3 \pm 2.1	6.8 \pm 3.5	27.4 \pm 6.9	27.5 \pm 5.4	22.8 \pm 11.4	18.0 \pm 9.7	13.8 \pm 4.1	17.8 \pm 1.0	0.2 \pm 0.3	1.8 \pm 0.3	9.1 \pm 1.4
Harvester trail	34.8 \pm 9.4	29.8 \pm 10.4	14.6 \pm 7.1	6.4 \pm 3.8 ^a	26.1 \pm 4.5	5.6 \pm 1.8	21.3 \pm 5.3	40.0 \pm 10.4	5.3 \pm 1.8	1.7 \pm 0.9	1.7 \pm 0.4	18.3 \pm 3.3

^a Tree canopy in harvester trails constitutes average cover estimates across the entire width of trails (i.e., estimates are derived from data in randomly located plots within trails to incorporate the forest edge influence, despite 0% harvest retention in the center of harvester trails).

was highly variable among sites (9.1 – 23.2%) and greatest in control forest outside of arenas. The greatest average soil moisture was in harvester trails (21%), presumably due to reduced transpiration. Leaf litter depth ranged from 1.4 – 2.5 cm, but was deepest in control and partial cuts (e.g., 2.4 and 2.5 cm within arenas, respectively) and < 1.8 cm in all trails (Table 2.3).

Discussion

Despite the well-established body of knowledge on the effects of even-aged silviculture on amphibian populations (e.g., deMaynadier and Hunter, 1999; Todd et al., 2014), there is still much to learn about effects on natal dispersal as part of a larger effort to document the ecological effects of the partial-harvesting practices that have become prevalent in the Acadian region (Thorpe and Thomas, 2007; Turner et al., 2013). Some prior studies suggest that many species decreased in abundance following high-intensity (30% retention) partial harvesting (Vanderwel et al., 2009; also *see* Steventon et al., 1998; Morneault et al., 2004; Tilghman et al., 2012). Thus, it is important to examine mechanistic links between the patterns of forest structure in partial harvests and consequent wildlife responses. In this study, we tested the initial and short-term dispersal orientation of juvenile wood frogs at the edge of heavy partial harvests (average: 30.4% retention, Table 2.3; nominal goal: 31-60%) to evaluate if dispersers would enter harvested areas. Overall, we observed greater proportions of individuals enter control forest than partial harvests, although the only difference that even approached significance was for selection of forest versus perpendicular-oriented trail. This pattern suggests that the vegetative structure and microclimatic regime of partially-harvested

stands are not as likely to be avoided by dispersing juveniles as clearcuts (e.g., deMaynadier and Hunter, 1995; Semlitsch et al., 2008).

Comparisons with prior studies of partial canopy removal and dispersing amphibians

In accord with several past studies of partial harvests and amphibians (e.g., Perkins and Hunter, 2006; Popescu et al., 2012a; Todd et al., 2014), our experimental animals showed little difference in the use of control and partial-cut treatments (Figure 2.3). For example, one study found similar abundances of western slimy salamanders (*Plethodon albagula*) in uncut control forest and partially-harvested forest with 60% stocking density retained (Hocking et al., 2012). Yet, a recent meta-analysis on the effects of timber harvest on terrestrial salamanders highlights the considerable variation in response: Tilghman and colleagues (2012) found that short-term population declines ranged from 29% in partial harvests (95% CI = -2% - 51% for 108 species and 24 studies) to 62% for clearcutting (95% CI = 29% - 80%). Thus, patterns of amphibian response to partial cutting are confounded by wide variation in harvest intensities (when reported, range: 30-70% canopy and 4 – 59 m²/ha basal-area retention; Tilghman et al., 2012). Our study occurred in heavy harvests with low canopy retention (average 30.4 %; Table 3.3), and the focus of our experiment on initial dispersal decision-making provided only a short-term window into behavior. Behavioral studies of individual movements across a range of harvest intensities will be critical for elucidating dispersal success and survival (Semlitsch et al., 2009), and responses may differ from studies of abundance. For example, in a study of the effects of partial canopy removal (~75% canopy retention)

on survival of ambystomatid salamanders in three regions of North America, Todd and colleagues (2014) found that adults survived as well or better in partially-harvested stands as in controls, but juvenile survival in partial harvests was significantly lower. Low juvenile survival in partially-cut stands could mean that they constitute an ecological trap if individuals in our study were willing to enter harvests but then suffered high mortality.

It is not surprising that by retaining some structural features of more mature forests, partial harvests may exhibit a weaker effect on populations than intensive clearcutting (e.g., Steventon et al., 1998; Semlitsch et al., 2009). However, empirical evidence suggests that there may be cumulative negative impacts of partial harvesting due to repeated-stand entries (e.g., Riechenbach and Sattler, 2007). In Virginia, the abundance of eastern red-backed salamanders (*Plethodon cinereus*) in partially-harvested stands declined twice, first after the initial shelterwood cut; then, after the population recovered, it was reduced a second time by an overstory removal cut 13 years later (Homyack and Haas, 2013). If amphibian populations cannot recover quickly between entries, partial-harvest methods that require multiple stand entries within a rotation may depress abundances on decadal scales, but responses may vary by species and region. For example, the interval estimated for recovery of salamander populations to pre-disturbance levels varied between 30-100 years in the Pacific Northwest (e.g., Karraker and Welsh 2006; Tilgman et al., 2013) and 25-70 years in the southern Appalachian region (e.g., Petranksa et al., 1993; Harper and Gynn, 1999).

Effects of partial-harvest landscape configuration on juvenile orientation

Consistent with predictions, our results suggest that the perpendicular trail orientation may represent a filter to juvenile movements (captures = 52:35 for forest vs. treatment; p -value almost significant at 0.068; Figure 2.3). If frogs rely on visual cues for orientation, animals may have perceived an increase in predation or desiccation risk when facing a perpendicular trail stretching away from them; this is consistent with prior evidence that dispersing amphibians can perceive forest habitat from at least 10 m away (Pittman and Semlitsch, 2013a) and a recent study of our target species suggesting that juveniles released in open cover may orient toward forest from 40-55 m away (Cline and Hunter, *in review*).

Prior studies also indicate that the spatial configuration of harvest edges may influence amphibian movements and diversity (Janin et al., 2012). For example, pool-exiting juvenile salamanders (*Ambystoma texanum*) and wood frogs exhibited non-random orientation influenced by the width and shape of surrounding forest (Walston and Mullin, 2008). At our sites, the harvest pattern resulted in a high perimeter-to-area ratio for strips within the stand (< 6 m wide skid trails; < 28 m wide residual strips) and two different configurations of edge to adjacent control forest: 1) where trails were perpendicular about 20% of the edge would be trail: forest; and 2) for parallel trails 100% of the edge would be trail: forest. Studies indicate that amphibians modify movements (i.e., willingness to enter habitats) in response to ground substrate (Semlitsch et al., 2013), habitat extent (Walston and Mullin, 2008), vegetation structure, microclimate (Rittenhouse et al., 2008), and physiological factors (Janin et al., 2012). Although longer-term studies of dispersers in partially-harvested forests are needed, our results

suggest that habitat selection may be influenced by the spatial configuration of logging trails and residual strips.

Potential effect of microclimate and microhabitat on edge effects and forest influence

It is well established that timber harvesting modifies microclimatic regimes for amphibians (Feder, 1983; Karraker and Welsh, 2006) and thus may affect orientation and habitat selection for dispersers (e.g., Baker et al., 2013). Given that partial harvesting reduces canopy cover overall and eliminates it completely in trails, we hypothesized that juveniles would avoid our treatments. Overall, our results suggest only limited links between humidity, temperature, and the ecophysiology associated with frog behavior (i.e., the willingness to enter partial harvests), since the microclimate regime of our treatments did not deter a significantly greater percentage of frogs from entering (with possible exception of the perpendicular-oriented trails). However, limited evidence suggests a possible link between microclimate and frog behavior: For example, frogs in the treatment side of arenas were captured first (59.2% by day 2, Figure 2.4) perhaps locomoting quickly due to risk of desiccation; in contrast, fewer were recaptured in the control by day two (46.6%), suggesting that it provided better habitat for temporary settling. Accordingly, we observed lower mean daily maximum temperatures at all levels in residual strip arenas (range: 30.7° - 33.9°) relative to trails.

Although microclimate appeared to play a limited role in frog behavior, the slight differences in preference for control forest among our treatments may be explained by differences in vegetation and ground cover (Table 2.3). As expected in the control forest,

we recorded higher levels of canopy cover (67.9% and 72.9% within and outside of arenas, respectively), leaf litter coverage (48.1% and 45.1%) and depth (2.4 and 2.1 cm), and low percentage of bare ground (6.7% and 0.3%; Table 2.3). In the arenas adjacent to residual strips, we recorded moderate levels of canopy (30.4% and 27.4%) and leaf litter coverage (45% and 27.5%) and depth (2.5 and 1.8 cm), and intermediate percentages of bare ground (0.7% and 17.8%), suggesting that frogs might find temporary refuge at this level of canopy retention. This contrasts sharply with the harvester trails, where we observed the lowest canopy cover (19.6% and 6.4% within and outside of arenas, respectively), leaf litter cover (22.2% and 26.1%) and depth (1.4 and 1.7 cm), and highest (or near highest) bare ground coverage (9.2% and 17.8%; Table 2.3) across the experiment.

Post-metamorphic orientation and juvenile ranging behavior

In our experiment, we focused on a short-term behavioral response – the initial habitat selection of dispersers – because dispersal potentially involves large-scale overland travel, when naïve frogs may rely primarily on proximate cues for deciding where to go (Pittman et al., 2014). Thus, individuals may be willing to enter open trails (0% cover) or residual strips even if they differ from preferred conditions for settlement (Cline and Hunter, 2014). Given our short time frame, we urge caution in extrapolating our results to adult life stages or other seasons when the behavioral context may involve prior experience, site fidelity, or non-random directionality (Walston and Mullin, 2008; Driscoll et al., 2013). Indeed, research suggests that use of partial harvests and subsequent survival may differ between adults and juveniles (*see* Table 3 in Popescu et

al., 2012a). In a study of the matrix permeability of open-canopy vegetation types, dispersing juvenile wood frog made forays > 30 m into treatments and then changed direction to return to forest (Cline and Hunter, 2014). In our study, animals showed little difference in the use of control and treatments; however, we constrained movement within 10 m and thus could not evaluate the ability of individuals to enter treatments, assess habitat, and change directionality. Longer-term tracking is needed to elucidate behavioral strategies (e.g., search mechanisms, relative velocities, path tortuosity) and to determine the scale over which decisions are made and the particular matrix types and configurations that might enable juveniles to disperse.

Management implications

Current forest practices in the Acadian forest region are creating unprecedented configurations of partial harvests (i.e., extensive strips of trails and logged matrix), and the effects of this spatial structure on wildlife populations remains relatively unknown (Fuller et al., 2004; Reichenbach and Sattler, 2007, Graham-Sauvé et al., 2013). Partial harvesting may result in increased: (1) forest edge and fragmentation; (2) harvester trail coverage; (3) variation in harvest intensity; and (4) frequency of stand entry (e.g., Baker et al., 2013), all of which may affect population connectivity. Our results indicate the relative permeability to juvenile frogs (willingness to enter) of three types of silvicultural edges; as such, it is among the first to empirically test individual behavior in partial harvests. Collectively, our three short-term measures of dispersal movements suggest that partially-harvested stands are not as likely to be avoided by dispersing juveniles as clearcuts. Perpendicular-oriented harvester trails may have decreased permeability to

juvenile movements relative to our other treatments (based on low willingness of individuals to enter). However, we also recognize that perpendicular trails may comprise only about 25% of available edge at the stand periphery in many cases, and longer term behavioral studies are necessary to elucidate dispersal outcomes. Ultimately, the habitat value of partially-harvested stands for pool-breeding amphibians will depend on if remnant populations and dispersing juveniles are capable of persisting and moving to new breeding sites across a complete cycle of harvests.

For forest managers, the goal of our study is to provide recommendations for harvest layout that both sustains timber production and conserves functional connectivity of amphibian populations across highly spatially-structured managed forests (e.g., partial harvests implemented in herring-bone patterns of strip cuts). Within the pool, amphibian reproductive effort (i.e., egg mass densities) has been shown to be positively associated with the amount of forest cover extending to 164 m from the pool edge (~ 65% reduction in egg masses in ponds surrounded by cut [70% removal] vs. uncut forest; Scheffers et al., 2013). Considering habitat connectivity beyond the pool, our initial findings imply that the spatial configuration of trails and residual strips may affect juvenile frog movements as they move from natal sites; thus, management should consider these patterns to retain canopy cover between breeding pools and adjacent terrestrial habitat (e.g., Popescu et al., 2012; Tilghman et al., 2012). This would start with an area immediately around the pool with very little or no harvesting (i.e., 25% limited harvest within the first 30 m of pool; 50% partial harvest within the subsequent 91 m) and from there the key issue would be how to arrange residual strips to facilitate emigration. As a

theoretical ideal, leaving residual strips like radiating spokes of a wheel, would allow frogs to travel away from the pool in multiple directions under continuous forest cover.

Given the realities of efficient harvesting operations and site factors, however, it would be more practical to consider the pool and immediately surrounding forest as a “node” of increased diameter within a partially-cut strip, thus allowing frogs to avoid machine trails and leave the pool in two directions (180° difference) under continuous cover of a harvested strip. Using this approach, managers could still maintain best management practices during harvest operations near vernal pools. For example, adequate canopy could be retained in the cumulative 122-m radius zone around a pool (Calhoun et al., 2005) by keeping trails narrow and widely spaced, and limiting harvests within the residual strips and the “node” surrounding each pool. Temporal issues could also be significant. Managers could extend the harvest over a greater number of entries (e.g., 3 or 4 per rotation instead of 2) to retain more structure and harvest during winter (i.e., outside of the dispersal window); however, the effects of increased re-entry frequency versus lower harvest intensity on amphibians is uncertain (Homyack and Haas, 2013).

Finally, predicting wildlife responses to partial harvesting is hindered by the dearth of direct, long-term studies of stand composition and structural changes over time (e.g., Saunders and Wagner, 2008; Bataineh et al., 2013), and the wide variation in practices underscores the need to develop a classification scheme to better describe harvest intensity, stand re-entry, and landscape configuration. The discrepancies among studies on the effects of partial harvesting on amphibians (Tilghman et al., 2012) may well be rooted in the wide variation in basal area retained (e.g., Vanderwel et al., 2009).

Further, few (if any) studies assess the ability of individuals to survive within harvested stands (*see* Todd et al., 2014), re-colonize regenerating partial harvests between entries (e.g., Homyack and Haas, 2009), or disperse. While our study suggests that landscape configuration may influence initial movements of dispersing amphibians, it is only a brief window into individual behavior. To conserve functional connectivity in landscapes where partial-harvest silviculture is predominant, we will need to integrate more refined classifications of harvest practices with studies of individual behavior (e.g., Bélisle 2005) across a range of harvest intensities and stand re-entries.

CHAPTER 3
MOVEMENT IN THE MATRIX: SUBSTRATES AND DISTANCE
TO FOREST EDGE AFFECT JUVENILE WOOD FROG
(*LITHOBATES SYLVATICUS*) DISPERSAL

Abstract

Population persistence often depends on functional connectivity for animals that transit multiple vegetation types to acquire resources, particularly for dispersers navigating a landscape matrix fragmented by agriculture, forestry, or urbanization. For many pool-breeding amphibian species, population viability depends on the ability of juveniles to locate and reach suitable habitat in the terrestrial matrix; identifying the scale and orientation of these movements is necessary to predict the consequences of landscape configuration for populations. We conducted two experiments to evaluate if different vegetation types alter the behavior of dispersing juvenile wood frogs (*Lithobates sylvaticus*). We measured the: (1) fine-scale movement (velocity, latency, path length, net displacement, path tortuosity, and orientation) of individuals (n = 150) released on five natural and anthropogenic substrates (asphalt, corn, forest leaf litter, hay, lawn); and (2) directionality of frogs (n = 168) released at different distances from forest in two open-cover types (lawns and hayfields). Using fluorescent powder to monitor movements, we mapped 318 paths. Movement performance differed: frogs demonstrated straighter paths, and greater net movements, path lengths, and velocities through treatments with lower structural complexity (asphalt > lawn > corn > forest leaf litter > hay). Frogs exhibited directionality toward forest in asphalt, lawn, and corn (random

orientation in forest control and hay). Juveniles in the second, distance-to-forest experiment exhibited differences in displacement and orientation attributed to treatment as well as direction and distance to forest edges. We observed more forest-oriented movement in lawn and random directionality in hayfields. Results indicate that the characteristics of the non-forest matrix may influence the ability of frogs to traverse open cover and orient toward forest from distances of at least 40-55 m. Thus, it is overly simplistic to assume movement performance is uniform across all matrix types, an important distinction because many landscape-population models use expert-based values that are a one-size-fits-all measure for open cover. Our study provides field-based, mechanistic approximations of dispersal that can be useful for predicting how the composition and configuration of the matrix might be managed to maintain or restore functional connectivity.

Introduction

Conservation strategies for many species use the patch-matrix model of landscapes (Forman, 1995) with the goal of maintaining patches of preferred habitat embedded in a matrix that allows some degree of connectivity among patches (Driscoll et al., 2013). Operationally, practitioners often focus on conserving patches but have little information on matrix quality; thus, they can only assume that the matrix is singularly inhospitable for even temporary settlement and that the size and spatial arrangement of the surrounding matrix will allow animals to access conserved patches (Kupfer et al., 2006; Prevedello and Vieira, 2010; Janin et al., 2012a). In reality, there may be a continuum of matrix conditions that vary as filters or conduits to movement, and the

quality of these cover types may influence the probability of an animal entering the matrix, the efficiency of movement, and dispersal success (Kuefler et al., 2010; Cline and Hunter, 2014). However, quantifying this variation in matrix quality remains a scientific and management challenge, in part because researchers need frameworks that integrate behavioral experiments with landscape-scale studies. The underpinning assumption is that successful movement depends on the characteristics of the matrix and how these interact with species-specific behavior (Bélisle, 2005; Haynes and Cronin, 2006; Burgess et al., 2012). Using this lens of behavioral landscape ecology, it then becomes possible to identify: (1) the probability of an animal entering the matrix (i.e., “willingness to enter,” e.g., Popescu and Hunter, 2011; Zeller et al., 2012); and (2) its subsequent (finer-scale) movement performance within each matrix type. Many modeling studies rely on expert-derived values to simulate connectivity (e.g., Hudgens et al., 2012), but these may be insufficient for adequately predicting the consequences of landscape configuration for population persistence.

It is widely understood that population viability is maintained by dispersal among breeding sites (Semlitsch, 2008); thus, the ongoing conversion of natural ecosystems to human-dominated land cover (Desrochers et al., 2011) amplifies the need to consider differential permeability of diverse cover types during dispersal. Studies suggest that matrix type can exert a strong influence on species movements. For example, sharp edges between habitat patches and matrix may decrease dispersal (i.e., a “fence” effect; Schtickzelle and Baguette, 2003; Nams, 2011), due to the perceived risk of predation upon entering an open-canopy cover type. However, the risk of predation may be mitigated if individuals move rapidly once edges are crossed. While a number of studies

have quantified the willingness of forest-dwelling species to enter open vegetation during dispersal (e.g., McDonough and Paton, 2006; Cosentino et al., 2011; Popescu and Hunter, 2011), much remains unknown about the mechanisms by which the matrix (directly or indirectly) influences individual behavior and the consequent distribution of patch-dependent species in fragmented landscapes (Driscoll et al., 2013).

Forest-dwelling amphibians are ideal taxa for this research because their movements occur at tractable scales and because many species have demonstrated sensitivity to habitat loss and fragmentation (deMaynadier and Hunter, 1998). Further, many species rely on aquatic and terrestrial habitat connectivity because juveniles typically emerge into the terrestrial environment from their natal pool following metamorphosis; some will emigrate to a new breeding pool (dispersal) while others return to breed in their natal pool (philopatry; Semlitsch, 2008; Clobert et al., 2009). Pittman and colleagues (2014) propose a unifying paradigm of juvenile amphibian movement in which dispersal is a multi-phase process during which individuals adjust movement and habitat responsiveness based on internal physiological state and environmental factors. Initially, juveniles are in an “away” mode to move from the pool edge, and they are probably relatively unresponsive to external cues such as microclimate or habitat structure. As juveniles become more responsive to habitat features, they enter a “directed” or ranging mode (Dingle, 1996; Barraquand and Benhamou, 2008), and they are likely to exhibit exploratory behavior at large spatial scales shaped by their ability to evaluate potential habitat from a distance (Bartoń et al., 2009; Pittman et al., 2014). Finally, individuals enter a “settlement” mode; searching for a suitable refuge, they likely respond to habitat features at very close range (Patrick et al., 2008). We hypothesize that

juveniles are most likely to cross boundaries and enter open-canopy vegetation types during the exploratory, directed movement phase, since they may orient to landscape features at scales greater than their very local or immediate range.

Prior amphibian dispersal studies in agricultural or urbanizing landscapes have focused on individual orientation (Vos et al., 2007; Pittman and Semlitsch, 2013a), resistance of the matrix to gene flow (Van Buskirk, 2012), or small-scale locomotor ability on different substrates without regard to landscape setting (e.g., Baughman and Todd, 2007; Semlitsch et al., 2012). Researchers have estimated the permeability of different open-canopy cover types to juvenile movements (e.g., Cline and Hunter, 2014), but none has paired these with measurements of fine-scale movement once matrix boundaries are crossed and in relation to landscape configuration (e.g., orientation to the nearest forest edge).

Study species and objectives

Our goal was to test whether different substrates and open-vegetation cover typically found in fragmented forest landscapes alter the behavior of juvenile amphibians during post-metamorphic movements. To accomplish this, we studied the wood frog (*Lithobates sylvaticus*) due to its widespread distribution in North America and its dependence on closed-canopy forest. This species avoids proximity to forest edges (deMaynadier and Hunter, 1998; Semlitsch et al., 2009) and is highly sensitive to forest removal (Cushman, 2006). Dispersal success (i.e., juveniles surviving to breed in new sites) is estimated at 18–20% (Berven and Grudzien, 1990), with mean net dispersal distances of 1140 ± 324 m for females and 1276 ± 435 m for males and maximum

distances of 2530 m (Semlitsch and Bodie, 2003). In contrast, movement estimates of post-breeding adults are an order of magnitude lower: 102-340 m (Baldwin et al., 2006) and > 300 m (Vasconcelos and Calhoun, 2004).

We conducted two experiments to measure: (1) fine-scale movements (velocity, latency, path length, net displacement, path tortuosity, and orientation) of individuals released on five substrates (asphalt, corn, forest leaf litter, hay, lawn); hereafter, *substrate experiment*; and (2) movement outcomes and directionality of individuals when released at different distances from forested corners in two open-cover types (lawns, hayfields); hereafter, *distance-to-forest experiment* (Figure 3.1). We undertook these experiments to extend a prior study in which permeability to wood frogs was estimated in clearcut, open-canopy and moderate-cover lawns, row crops, and hayfields (permeability: row crop < hayfield < clearcut < open lawn < moderate-cover lawn; Cline and Hunter, 2014). In this study, we refine these population-level permeability estimates with detailed measurements of fine-scale movements by individuals. Our guiding hypothesis was that movement performance would differ among treatments due to structural differences in cover, refuge availability, and physical impediments to locomotion.

Predictions for post-metamorphic movements and orientation

Prior to our experiments, we predicted that five environmental factors (i.e., vegetation structure, microclimate, food, conspecifics, and predators) might influence observed juvenile movement performance. Amphibians have been shown to alter movement behavior in response to habitat extent (Rothermel and Semlitsch, 2002), substrate (Baughmann and Todd, 2007; Semlitsch et al., 2012), vegetation structure

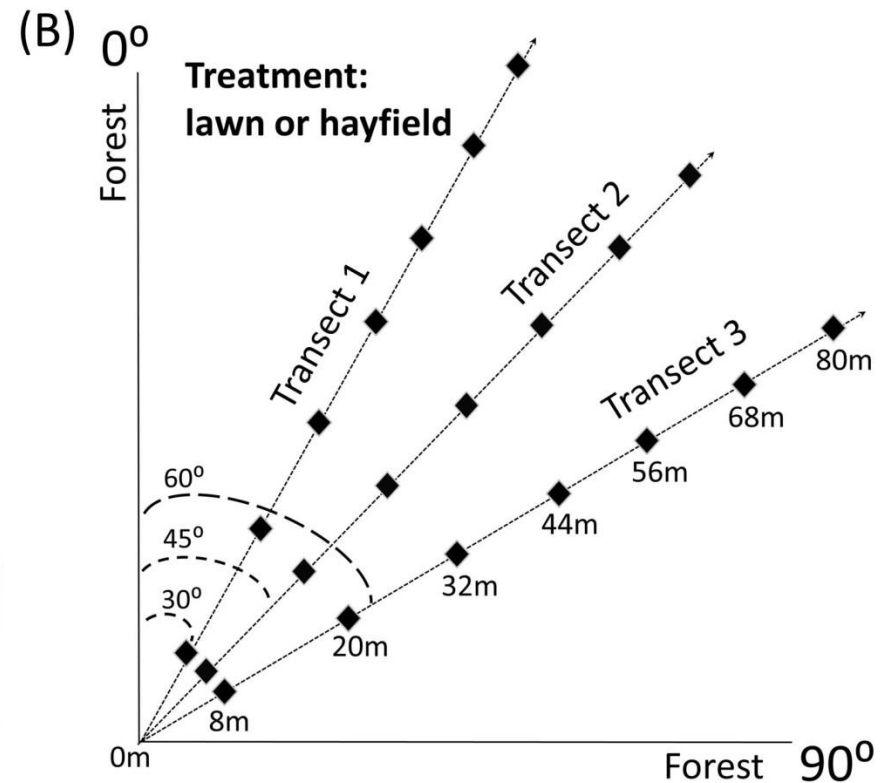
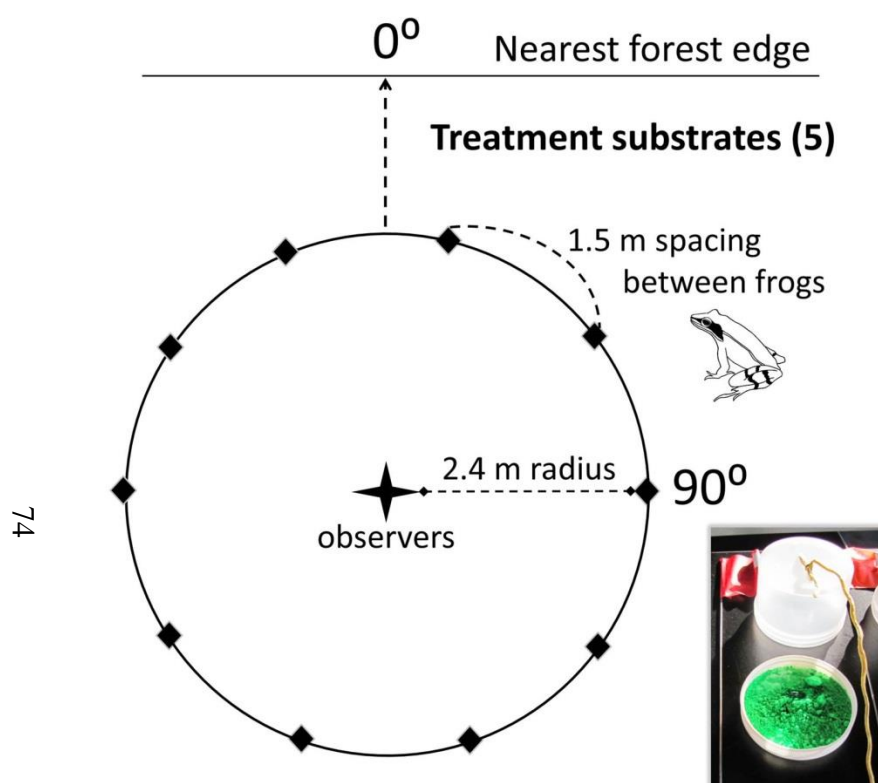


Figure 3.1. Experimental design for evaluating the movement of juvenile *L. sylvaticus* in: (A) five substrates (asphalt, corn, forest leaf litter, hay, lawn); and (B) two open-cover vegetation types during dispersal. Panel (A) depicts the substrate experiment design constituting a 2.4 m radius arena; diamonds indicate where ten frogs were simultaneously released and tracked (see embedded photo of remote release mechanism: inverted cup, fluorescent powder, and string). Panel (B) depicts the design for distance-to-forest experiment: three transects emanating (30°, 45°, and 60°, respectively) from an ~90° interface of two straight forest edges creating a corner framing lawn or hayfield. Along each 80 m transect frogs were released at seven 12 m intervals. (*Note:* figure not to scale).

(Stevens et al., 2004), physiological stress factors (Janin et al., 2012b), microclimate (Rittenhouse et al., 2008), and predation risk (Pittman et al., 2013b). We speculated that frogs in our study were largely in a directed mode: individuals had already departed their natal pool and would exhibit exploratory movements in search of food, cover, ease of locomotion, and appropriate microclimate. We assumed they were not yet made in settlement mode.

In our substrate experiment, we predicted that velocity, path length, and net displacement of individual movements would be greater in substrates with less structural complexity (asphalt, lawn, perhaps corn) because these would directly impede locomotion less. We anticipated that path tortuosity (i.e., the sinuosity of movement) would be greater in substrates with more structural complexity (forest litter, hay, perhaps corn) and thus cool moist microclimates or cover. We further predicted that the time to first movement following release (latency period) would be greater in substrates with more settling habitat (forest litter) and physical cover (hay, corn) if frogs perceived these as a refuge from thermal stress or predators. We expected that directionality would be random in forest (i.e., ample preferred habitat) and perhaps hay (where thick vegetation provides cover and may restrict the ability to see a distant forest), but that frogs would orient toward the nearest forest when the edge contrast was stark (lawn, asphalt, corn).

In the distance-to-forest experiment, we predicted that net displacement would be greater in lawns than hayfields, where thick vegetation may limit locomotion. Similarly, we predicted that frogs released farther from the forest edge would be less able to detect the edge and thus would move relatively shorter distances. Finally, we expected that directionality in hayfields would be random at all but the shortest distances to forest edge

(e.g., < 10-15 m; Rothermel and Semlitsch, 2002; Pittman and Semlitsch, 2013a) due to decreased visual range toward a subtler edge. In contrast, we predicted that juveniles in lawns would exhibit greater forest-oriented directionality overall; especially at greater distances (e.g., > 35 m; Cline and Hunter, 2014) due to wider visual range toward a stark edge.

Materials and Methods

Study sites

Our study was conducted in Penobscot County, Maine, USA on University of Maine lands (Demeritt Forest, Witter Farm, athletic fields, and parking lots) and the Penobscot Valley Country Club (44°51'41.87" N, 68°41'14.42" W). In the lower Penobscot River watershed (9,974 km²), anthropogenic landscape fragmentation involves forestry, and to a lesser degree, residential development, and agricultural practices (i.e., 78.3% of the landscape is forested, of which 20.4% has been recently cut; 3.9% is urban; 3.9% is agriculture, and the remainder comprises freshwater bodies).

We selected five treatments for the substrate experiment: asphalt, regularly cut lawn, forest leaf litter; a row crop (silage corn); and unmowed or recently mowed hay. We selected reasonably flat surfaces to avoid slope and aspect bias and used each location only once. Treatment patches averaged 3.44 ± 0.43 hectares in size and were abutted by at least one forest edge ≥ 135 m long (with the exception of forest controls). Locations for all trials were 35-40 m from the nearest forest edge. For the distance-to-forest experiment, we selected locations where an $\sim 90^\circ$ interface of two straight forest edges (range of lengths: 135-295 m) created a corner framing a lawn (N = 4) or an uncut

hayfield (2 sites, used twice; see *Experimental design* and Figure 3.1B). We avoided slope bias (by using flat areas) and directional bias (by selecting corners facing different cardinal directions).

Vegetation characteristics for all treatments were recorded in July-Aug 2013. Asphalt treatments consisted of 100% impervious surface with 0% canopy cover with forest along at least one edge and residential or campus land-uses in other directions. Hayfields constituted a mixture of grasses and legumes, with average stem height of 1.1 m; mowing and baling occurred on 17 July but there were no differences in observed movements before or after that date (per analyses by trial date described below). Lawn treatments were exotic grasses mowed once per week to retain an average stem height of 10.3 ± 0.23 cm. Row crop treatments (hereafter *corn*) comprised feed corn sown in mid-May; inter-row distance averaged 0.95 ± 0.16 m, and the substrate underneath corn stalks consisted of bare tilled soil, interspersed with weeds. Forested controls (not recently harvested; natural regenerated with ~ 75% canopy cover) were characterized by mature mixed coniferous and deciduous forest. Ground cover was undisturbed and characterized by leaf litter interspersed with rocks, coarse woody debris, moss, and lichen, and a fairly consistent herb layer (hereafter *forest*).

Experimental design

Our substrate experiment was performed in a circular release scheme (Figure 3.1A) constituting a 4.8 m diameter open area in which two observers were positioned centrally (back-to-back) to record the initial movement behavior and directionality of juveniles released at fixed-interval locations along the circle (i.e., 10 individuals spaced

at 1.5 m intervals along the 15.1 m circumference). We released frogs simultaneously ~ 5-8 minutes after sunset and tracked their movements using fluorescent powder and black light over the subsequent night ($n = 10$ frogs per trial in three replicates of five treatments, for a total of $n = 150$ tracked; Figure 3.1A). Our substrate trials occurred on 15 dates during the height of post-metamorphic dispersal in July 2013 (replicate 1: 6-10 Jul; replicate 2: 13-17 Jul; replicate 3: 21-24 and 28 Jul). The substrate surface surrounding each release container was sprayed with well water just before each trial to eliminate differences in moisture-holding capacity of the different substrates (Semlitsch et al., 2012). Thus, we intended to induce similar experimental conditions (i.e., microclimate) for the initial break of latency for each frog in each substrate.

Frog release containers consisted of an inverted opaque plastic container (SKS Bottle & Packaging, Inc., Watervliet, NY, USA; model 0610-08: 8.5 cm diameter x 6.6 cm height) with two ventilation holes, containing one of our 10 different color fluorescent powders (Figure 3.1A). Powder tracking techniques have been widely applied in herpetological studies; these pigments are harmless to amphibian skin (Eggert, 2002; Rittenhouse et al., 2006) and degrade when exposed to water and weather. The powders were mixed with mineral oil in a 40:1 ratio of powder to oil so that each frog would “self-coat” with the powder prior to release. We used an ECO series of powders, composed of a polymer free of carcinogens, formaldehyde, or other toxins (DayGlo Color Corp, Cleveland, OH, USA). Each release container was inverted on its lid and connected to string that extended to the center of the release circle and allowed observers to open all 10 containers remotely simultaneously.

Following a 15-min acclimation period (Turchin, 1998), frogs were released and observers recorded time to first movement; after break of latency, frogs were left to traverse each substrate without interference for a period of 60-90 minutes (Semlitsch et al., 2012) and we observed them using only black lights (Inova X5 ultraviolet LED: 365-400 nm). If all frogs had departed release locations after the initial 60 minutes, two observers would approach and begin mapping two of the 10 frog paths; we would delay tracking up to an additional 30 minutes if latency was still unbroken for \geq two frogs. The order of tracking was determined randomly for the first frog and observer; the second observer would begin at an interval of five release locations away (e.g., if frog three was selected at random, the second observer would begin tracking frog eight). Researchers moved along each path slowly and quietly, extending a length of fluorescent string along the frog's path as indicated by a trail of powder (until the frog was observed visually or path deteriorated). Each frog's stopping location was marked with a wire flag, and the time required for it to move to its final location was recorded to calculate velocity. Our goal was to obtain five movement metrics for each frog after the break of latency: (1) net displacement (m), or the straight-line distance from start to end location; (2) total path length (m), or the length of string extended along the exact path; (3) velocity (cm/s), or the net distance / total time spent moving; (4) path tortuosity (= net displacement / total path length); and (5) directionality (azimuth from start to end location, $^{\circ}$). We used directionality measures to derive each frog's orientation relative to the nearest forest edge (except in the forested control, where an edge with open-cover was > 125 m away and we assumed orientation would be random).

We conducted our distance-to-forest experiment using a landscape configuration of roughly a $\sim 90^\circ$ interface of two straight forest edges creating a corner framing a lawn or hayfield (Figure 3.1B). At each lawn or hayfield site, we delineated three transects (30° , 45° , and 60° from one edge at each corner); each transect constituted an 80 m vector along which seven frogs were released at evenly spaced intervals (8, 20, 32, 44, 56, 68, and 80 m from corner) and subsequently tracked using powder and black light. Distance-to-forest trials occurred over four consecutive nights (31 Jul, 1-3 Aug 2013); we conducted simultaneous trials in paired lawn and hayfield sites on each date ($n = 21$ frogs per trial with two treatments and four replicates, for a total of $n = 168$ tracked). We used the same “powder” release containers described above. Following release (~ 5 -8 min after sunset), all frogs were permitted to transit at will until 2:00 AM, when observers would return to map frog paths using black light and obtain the following metrics: (1) net displacement (m); and (2) directionality from frog start to end location, which we later used to derive individual frog orientation relative to the nearest forest edge(s) at each site.

Juvenile amphibian rearing and release

Prior to our experiments, metamorph frogs were reared by collecting eggs from natural vernal pools, roadside ditches, and skidder ruts in Penobscot County, ME and raising larvae in artificial pools using methods described in chapter one and published in Cline and Hunter (2014). Before each release, we measured (snout-vent length [SVL]: mm; weight: g), marked (one of 10 fluorescent powder colors in release cup), and randomly assigned frogs to one of our study sites and treatments. At the conclusion of

trials, each frog was collected (if observed at path end) and returned to a forested location within 50-100 m of its natal pool.

Microclimate and habitat sampling

We collected temperature (°C) and relative humidity (%) in our substrate experiment using iButton data loggers (Maxim, Inc., Dallas Texas, USA). Within each substrate and cover type across all study site replicates, we measured temperature and humidity at 1-minute intervals at: (1) ground-level within each release circle; and (2) under thermal refugia located 15 m outside of the circle (i.e., 5–8 cm below coarse woody material in forest, under root masses in hay, etc.) to represent potential cover for a dispersing frog. We also collected microhabitat data, characterizing vegetation in terms of ground cover, canopy closure (using densitometer), vegetation height, stem density, and inter-row distance (corn). We estimated ground cover as the percentage of 3 x 3 m plots classified as: leaf litter, moss / lichen, herbaceous, slash, bare soil, and rocks. Habitat characteristics of the hayfield, cornfield, and lawn were collected three times (July 12-13, 17-18, and 22-25) to account for vegetation growth.

Data analysis and statistical approach

Each frog was used once at one location, and thus constituted our experimental unit of analysis. In the descriptions that follow, the comparisons of movement path parameters includes both the substrate and distance-to-forest experiments.

We compared the mean net displacement, latency, path tortuosity, path length, and velocity of movement paths among treatments using a one-way analysis of variance

with treatment as the main effect (ANOVA, R package [*car*]; Fox & Weisberg 2011). We log transformed net displacement, latency, and velocity to achieve normality in our data distributions prior to each analysis; path tortuosity is presented on a scale of 0-1 (greater values indicate straighter paths). When ANOVA tests proved significant, we performed Tukey's honestly significant differences (HSD) test to investigate pairwise dissimilarity between treatments while controlling for multiple comparisons. Correlations of frog size versus movement responses were performed using Pearson's simple correlations. We investigated possible additive effects of transect and frog start location in our distance-to-forest experiment using a two-way ANOVA.

For juvenile orientation, we used circular statistics to test if individuals moved toward the nearest forest edge. Orientations were standardized so that 0° represented the nearest forest edge(s) adjacent to treatments for all release sites and trials. We used Rayleigh's test of uniformity (general unimodal alternative with unknown mean direction and vector length) to determine whether orientation deviated significantly from a random distribution for each treatment, transect, or distance (Fisher, 1993). To test if frog movement deviated significantly from a hypothesized mean angle (i.e., the bearing toward the nearest forest edge), we used a V-test and a Rayleigh test of uniformity with specified mean direction. We analyzed orientation propensity for animals that moved > 0.1 m from initial release locations.

We assessed potential differences in the size of metamorphs (SVL) released among treatments, trial dates, transects, or frog start locations in each experiment separately using a one-way ANOVA. All ANOVAs and Tukey's HSD tests were conducted in Program R (version 2.15.3; R Development Core Team, 2013). Circular

statistics were conducted in Program R (R packages [*CircStats*]: Jammalamadaka and Sengupta 2001; and [*circular*]: Lund and Agostinelli, 2013), and Oriana (version 3: Kovach Computing Services; Anglesey, Wales, UK, 2014). Circular histograms were created using Rose.Net (version 0.10.0.0, Todd A. Thompson Software, 2012). All statistical tests were deemed significant at $P < 0.05$.

Results

We quantified significant differences in the fine-scale movements of juvenile *L. sylvaticus* when released in natural and anthropogenic substrates (asphalt, lawn, forest, corn, hay) and at varying distances from forest edges using six metrics (velocity, latency, path length, net displacement, path tortuosity, and orientation).

The average SVL of juveniles in the substrate experiment was 16.59 ± 0.11 mm with no significant differences among treatments ($F_{4,145} = 0.51$, p -value = 0.74; ANOVA; Tukey's HSD). However, metamorphs released later in the season (i.e., trial 3: 21-28 Jul 2013; 15.71 ± 0.17 mm) were significantly smaller than those released during trial one (6-10 Jul; 17.42 ± 0.19 mm) or two (13-17 Jul; 16.62 ± 0.14 mm; $F_{1,148} = 51.59$, p -value < 0.001). The overall average mass was 0.55 ± 0.02 g and tracked the same pattern observed for SVL. In the distance-to-forest experiment, the average SVL of juveniles was 14.11 ± 0.09 mm, with no differences among treatments (Welch two sample t -test: $t = -0.53$, $P = 0.31$) or trials ($F_{1,166} = 3.73$, $P = 0.06$). We released 150 metamorphs (30 on each substrate type) in the substrate experiment, mapped all their powder trails, and visually relocated 89% (Table 3.1). In the distance-to-forest experiment, we released 168

Table 3.1. Movement metrics for frogs released and relocated in: (1) five substrate types across two sites and three trials per substrate (first six rows of data); and (2) distance-to-forest experiment in lawns and hayfields across six sites and four trials (final three rows).

See Appendix 1 for the breakdown of distance-to-forest results by trial and transect.

1. Substrate	# Released	Observed at path end	% paths > 1 m	Total path length (m)*	Net displacement (m)*	Range path length (m)
				Mean \pm SE	Mean \pm SE	
Asphalt	30	26	100.0	39.50 \pm 3.81 ^A	26.10 \pm 2.69 ^A	5.57 - 106.35
Lawn	30	23	86.7	9.37 \pm 1.87 ^{AB}	5.12 \pm 0.88 ^{AB}	0.70 - 43.07
Forest	30	25	90.0	9.44 \pm 2.11 ^{AB}	5.33 \pm 1.16 ^{AB}	0.59 - 38.20
Corn	30	29	86.7	6.02 \pm 1.25 ^{AB}	3.60 \pm 0.86 ^{AB}	0.34 - 33.12
Hay	30	30	70.0	2.18 \pm 0.47 ^B	1.24 \pm 0.35 ^B	0.27 - 14.67
Total	150	133	88.0	13.30 \pm 1.47	8.28 \pm 0.97	0.27 - 106.35
2. Matrix type						Range net displacement (m)
Lawn	84	62	34.5	...	2.18 \pm 0.42 **	0.00 - 19.95
Hayfield	84	62	13.1	...	0.73 \pm 0.20 **	0.00 - 14.88
Total	168	124	23.8	...	1.46 \pm 0.24	0.00 - 19.95

* These metrics varied significantly by treatment (ANOVA; $F_{4, 145} = 38.06$; $P < 0.0001$); superscript letters indicate significant differences among groups after controlling for multiple comparisons (Tukey's post hoc HSD at $\alpha \leq 0.01$).

** Net displacement varied significantly by treatment (ANOVA; $F_{1, 166} = 14.38$; $P < 0.0001$). Path length was not measured in distance-to-forest experiment.

metamorphs (84 in each matrix type), mapped all their powder trails, and visually relocated 74% (Table 3.1 and Appendix C).

Substrate experiment

As hypothesized, fine-scale movement performance differed significantly among substrates: frogs demonstrated significantly greater net movements ($F_{4, 145} = 38.06$, $P < 0.001$; Figure 3.2A) and total path lengths ($F_{4, 145} = 39.38$, $P < 0.0001$; Table 3.1), straighter paths (path tortuosity: $F_{4, 145} = 3.23$, $P = 0.01$; Figure 3.2C), and faster rates of movement (velocity: $F_{4, 145} = 26.34$, $P < 0.001$; Figure 3.2D) through treatments with the least structural complexity (overall trend: asphalt > lawn > corn > forest > hay; Figure 3.2). We observed that frogs on pavement exhibited significantly straighter movement trajectories (0.76 ± 0.03 vs. 0.59 ± 0.14 ; $P = 0.007$), net displacements (26.10 ± 2.69 m vs. 1.24 ± 0.35 ; $P < 0.0001$), and velocity (0.76 ± 0.08 cm/s vs. 0.08 ± 0.01 cm/s; $P < 0.0001$, Figure 3.2) than frogs on hay (Tukey's HSD test). We failed to detect significant differences in latency among substrates ($F_{4, 145} = 2.04$, $P < 0.09$) due to high variability within treatments. Average latency was longest in the lawn and asphalt (208 ± 50 s and 173 ± 51 s, respectively), intermediate in the corn (123 ± 61 s), and shortest in the hay and forest (94 ± 31 s and 61 ± 13 s; Figure 3.2B). We found scant evidence of a correlation between frog size (weight or SVL) and any movement response; the strongest relationship was between latency and body length in lawn ($y = 391.05 x^{2.67}$; $R^2 = 0.29$).

As outlined in our predictions, we observed strong target-oriented movement toward the nearest forest edge in our most open cover types (asphalt > lawn > corn), corroborating our prediction (Figure 3.3; asphalt: Rayleigh's (R-test): $P = 0.09$; V-test:

Figure 3.2. The observed movement behavior of *L. sylvaticus* ($n = 150$) during releases in five types of substrate. Panels depict: (A) net distance traveled (m); (B) latency (i.e., the time from release to first movement in s); (C) path tortuosity (net distance / total path length); and (D) velocity (cm/s, based on total path length). All responses were log transformed to achieve normality except tortuosity (scale 0-1: greater values indicate straighter paths). Reported significance values (global tests of treatment effect) are from analyses of variance (ANOVA); letters A and B indicate similarity or dissimilarity among substrates after controlling for multiple comparisons (Tukey's post hoc HSD $\alpha \leq 0.01$).

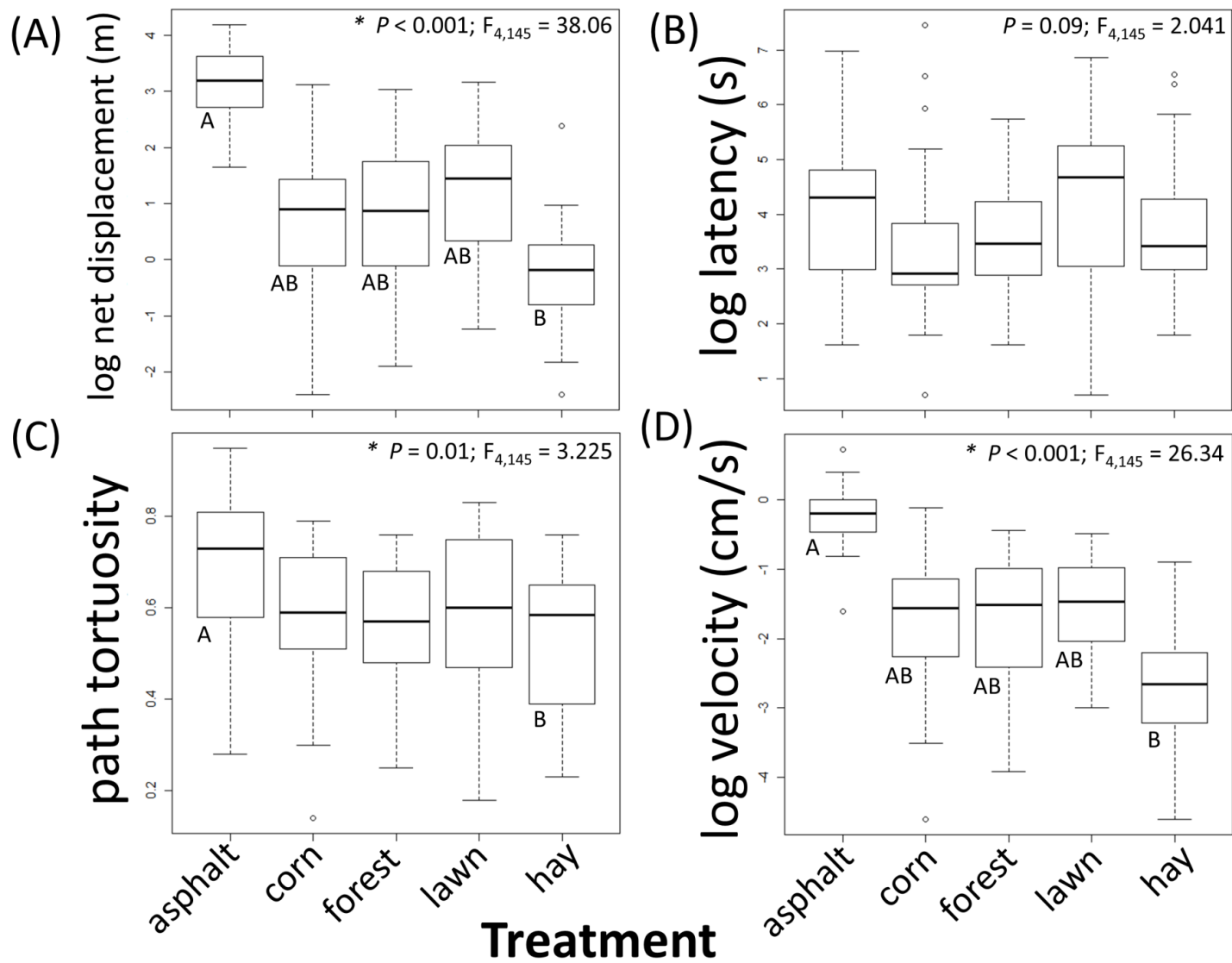
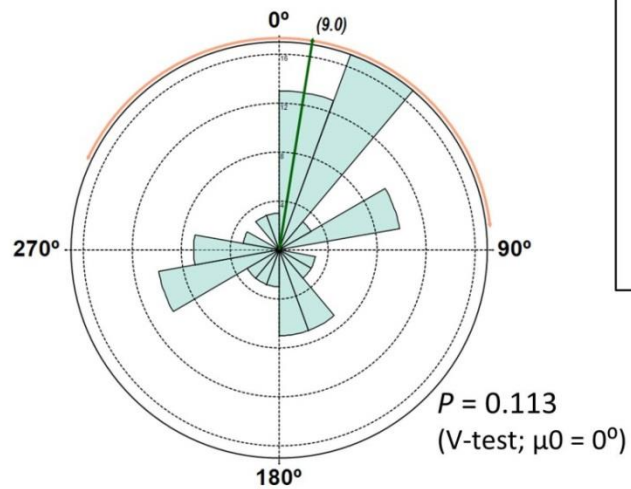


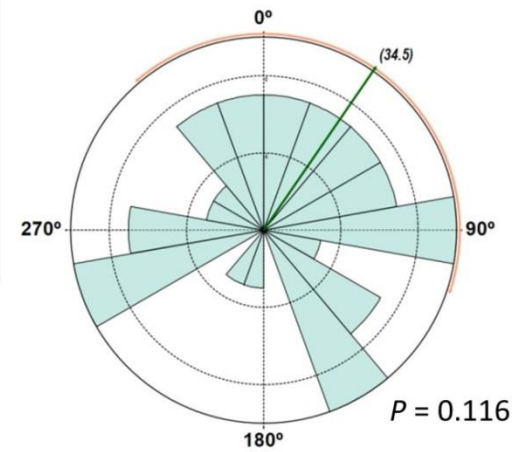
Figure 3.3. Orientation of *L. sylvaticus* (n = 150) during experimental releases in five types of substrate. Orientations were standardized so that 0° represents the nearest forest edges (range: 35-40 m away). Bold solid lines indicate the mean direction of all frogs released in that substrate (mean direction in parentheses) and the length of the wedges represents the percentage of animals (5% increments) with orientations that fell within the designated 20° bin (standard deviations indicated by arcs external to each circular histogram). Asterisks indicate treatments in which frogs demonstrated statistically significant directionality toward the nearest forest edge(s) according to a Rayleigh Test of Uniformity with specified mean direction ($\mu_0 = 0^\circ$).

Control: forest

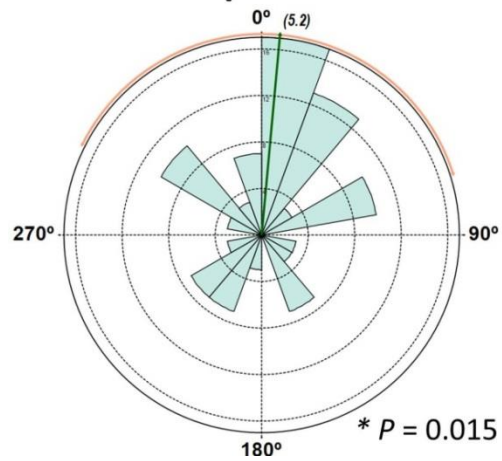


↑ 0° = dir
of nearest
forest
edge

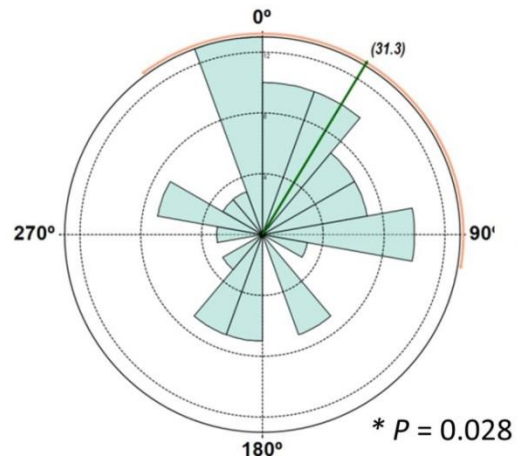
hay



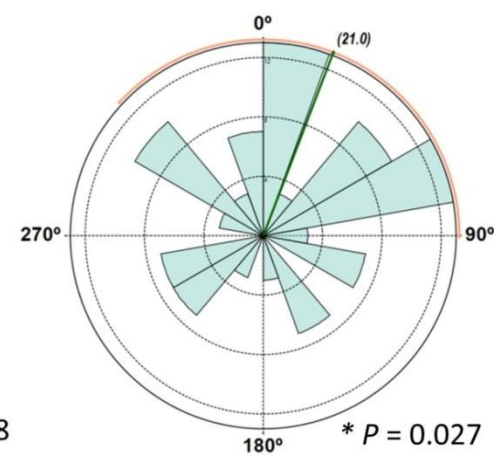
asphalt



corn



lawn



$P = 0.01$; lawn: R-test: $P = 0.12$; V-test: $P = 0.03$; corn: R-test: $P = 0.08$; V-test: $P = 0.03$). We observed random (non-target-oriented) directionality in the control forest where there may be ample preferred settling habitat (R-test: $P = 0.47$; V-test: $P = 0.11$) as well as in the hay (R-test: $P = 0.56$; V-test: $P = 0.12$), supporting our hypothesis that greater structure may impede detection of forest at 40 m distances (Figure 3.3).

During our substrate experiment, microclimates were relatively cool and moist at night in most substrates (e.g., 19-29°C and > 45-99% relative humidity, Figure 3.4), but reached potentially lethal daytime temperatures (35°C and 31°C within refugia in the asphalt and lawn, respectively), after 14:00 hours. Notably, during nocturnal trials (19:00 – 24:00 h; Figure 3.4A), temperatures ranged widely in the forest (~19°C Δ in temperature) and asphalt (almost 30°C Δ in temperature) and humidity fluctuated from 43-98% (Figure 3.4A; also see inset for nocturnal period in Figure 3.4B). In plausible frog refugia locations, the hay, corn, and forest treatments consistently demonstrated the most benign microclimates (15.5 – 26.8°C; 60-99%; Figure 3.4B).

Distance-to-forest experiment

Frogs released in the distance-to-forest experiment exhibited differences in net displacement and directionality that could be attributed to treatment (lawn, hayfield) as well as direction and distance to the nearest forest edge (see Figure 3.1B for transect design). First, patterns of net displacement corroborated the substrate experiment: average net displacement varied significantly ($F_{1, 166} = 14.38$, $P < 0.001$; Figure 3.5A), with far greater movement in lawns (2.18 ± 0.42 m, comparable to 5.12 ± 0.88 m in substrate experiment) than hayfields (0.73 ± 0.20 m vs. 1.24 ± 0.35 m in substrate

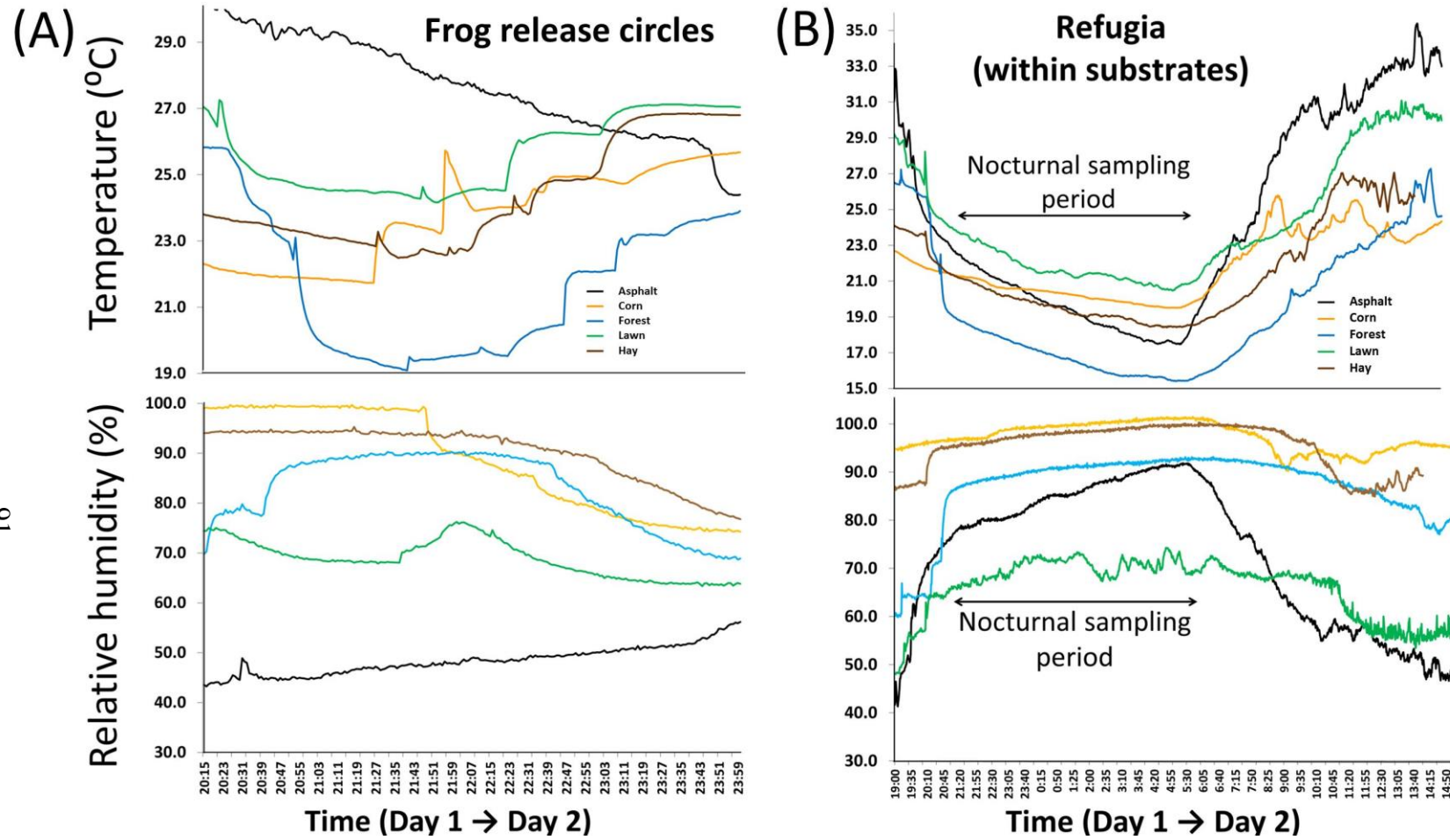


Figure 3.4. Temperatures (°C) and relative humidity (%) of five substrates averaged across 21 days (6-26 July) during substrate experiment. Panel (A) depicts microclimate for random surface locations within the 2.4 m radius release circle and panel (B) illustrates the microclimate at potential refugia within each substrate. Data are compiled from time of release through the conclusion of tracking on the subsequent day. Note the difference in scale for panels (A) and (B).

experiment). Net displacement ranged from 0-19.95 m and varied by treatment ($F_{1, 166} = 4.37$, $P = 0.04$), but not by transect (30° , 45° , 60° : $F_{2, 165} = 0.59$, $P = 0.56$; Appendix D). The combined effects of distance and direction to forest (i.e., transect and frog start distance) did not significantly influence the scale of movement ($F_{8, 159} = 1.60$, $P = 0.13$); although there was a possible trend of increased displacement at greater distances (Appendix D).

As hypothesized, the orientation of juveniles toward the nearest forest edge differed by treatment and distance from the edge (Figure 3.5, Appendix E). On the lawn, frogs moved toward forest from transects 1 and 3 but not from the middle transect (T1: V-test: $P < 0.01$; T3: $P = 0.02$; Figure 3.5A). In contrast, frogs exhibited random orientation on transect 1 and 3 in the hayfield (T1: $P = 0.59$; T3: $P = 0.24$), and moderate directionality toward one of the forest edges (180° but not 270°) along the middle transect (T2: V-test [$\mu 0$] = 180° or 270° : $P = 0.03$ and 0.35 ; Table 3.2, Figure 3.5B).

Distance to forest also influenced orientation (Table 3.2, Appendix E), although patterns are less clear. Juveniles in the lawn demonstrated strong directionality toward forest at shorter release distances (8-44m) along Transect 1 and 3 (T1: V-test: $P = 0.03$; T3: V-test: $P = 0.05$; Table 3.2); as expected, this effect was decreased at more distant locations (56-80m) along all three lawn transects (T1: V-test: $P = 0.067$; T2: V-test [$\mu 0$] = 180° or 270° : $P = 0.069$ and 0.84 ; T3: V-test: $P = 0.062$; Table 3.2, Appendix EA). In contrast, hayfield frogs only exhibited strong target-oriented movement at the near stations on transects 2 and 3 (T2: V-test [$\mu 0$] = 180° or 270° : $P = 0.02$ and 0.58 ; T3: V-test: $P = 0.01$, Table 3.2) and the 56-80 m distance classes on transect 1 (T1: V-test: $P = 0.04$; Table 3.2, Appendix EB).

Figure 3.5. Orientation of *L. sylvaticus* ($n = 168$) released along three transects emanating from forest corners (i.e., $\sim 90^\circ$ interface of contiguous forest and open-canopy vegetation) in: (A) lawns; (B) hayfields. Along each 80 m transect frogs were released at seven 12 m intervals. Symbols, significance tests, and notation in the circular rose diagrams are parallel in structure to Figure 3.3 (*see* legend). The directions of nearest forest edge(s) are: (1) 270° for Transect 1; (2) equidistant to 180° and 270° for Transect 2; and (3) 180° for Transect 3.

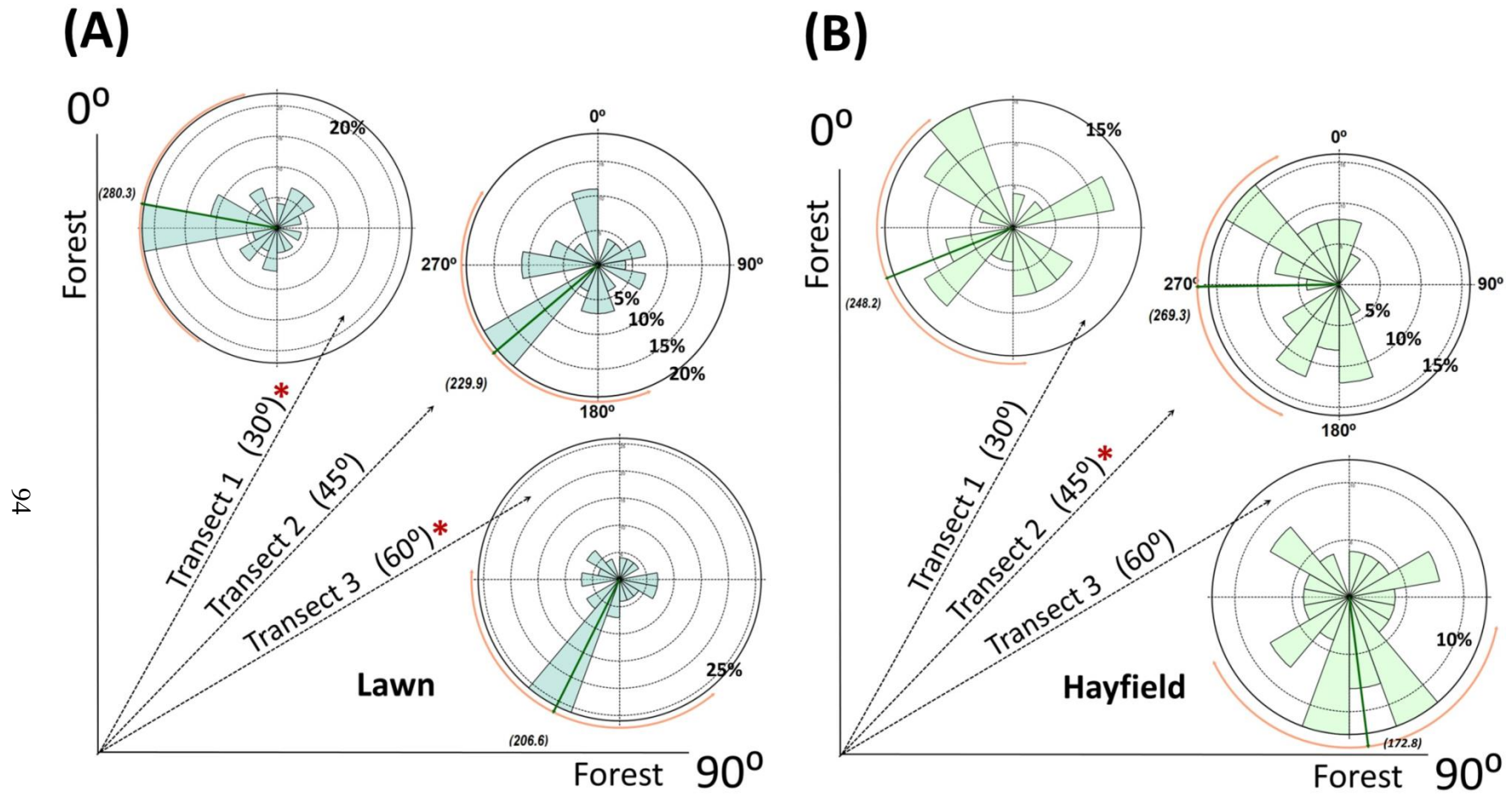


Figure 3.5(A) Lawns. **Transect 1:** Rayleigh's test: $P = 0.050$; V-test ($\mu_0 = 270^\circ$): $P = 0.008$, $n = 27$; **Transect 2:** Rayleigh's test: $P = 0.399$; V-test ($\mu_0 = 180^\circ$ or 270°): $P = 0.087$ and 0.150 , $n = 27$; **Transect 3:** Rayleigh's test: $P = 0.065$; V-test ($\mu_0 = 180^\circ$): $P = 0.019$, $n = 27$.

Figure 3.5(B) Hayfields. **Transect 1:** Rayleigh's test: $P = 0.548$; V-test ($\mu_0 = 270^\circ$): $P = 0.588$, $n = 26$; **Transect 2:** Rayleigh's test: $P = 0.057$; V-test ($\mu_0 = 180^\circ$ or 270°): $P = 0.349$ and 0.027 , $n = 25$; **Transect 3:** Rayleigh's test: $P = 0.348$; V-test ($\mu_0 = 180^\circ$): $P = 0.237$, $n = 25$.

Table 3.2. Analysis of *L. sylvaticus* orientation in distance-to-forest experiment.

Treatment	Transect (°)	Distance class (m)	Sample size	Mean direction (°)	SD (°)	Vector magnitude	Consistency ratio (r)	Rayleigh's Test (R-Test) [†]	Test of Uniformity: Specified mean dir (V-Test) [‡]
Lawn	30° (1)	All	27	280.3	66.3	8.94	0.33	0.050**	0.008**
	45° (2)	All	27	229.9	73.1	5.00	0.19	0.399	(1) 0.087; (2) 0.150
	60° (3)	All	27	206.6	66.9	8.55	0.32	0.065*	0.0190**
Hayfield	30° (1)	All	26	248.2	76.4	3.01	0.11	0.548	0.588
	45° (2)	All	25	269.3	66.0	8.42	0.34	0.057**	(1) 0.027**; (2) 0.349
	60° (3)	All	25	172.8	72.2	5.16	0.21	0.348	0.237
Lawn	1	Class 1 (8, 20, 32, 44)	15	305.0	61.9	6.24	0.42	0.072*	0.031**
	1	Class 2 (56, 68, 80)	12	241.8	65.4	4.18	0.35	0.237	0.067*
	2	Class 1	16	255.2	76.8	1.61	0.10	0.854	(1) 0.301; (2) 0.518
	2	Class 2	11	218.9	66.4	3.61	0.33	0.312	(1) 0.069*; (2) 0.841
	3	1	15	199.4	67.3	4.65	0.31	0.240	0.055*
	3	2	12	214.9	66.3	3.97	0.33	0.274	0.062*
Hayfield	1	1	15	34.1	78.7	0.86	0.06	0.953	0.412
	1	2	11	242.3	61.2	4.72	0.43	0.132	0.037*
	2	1	15	254.0	63.5	5.78	0.39	0.107	(1) 0.024**; (2) 0.584
	2	2	10	297.4	66.7	3.23	0.32	0.362	(1) 0.268; (2) 0.193
	3	1	13	179.8	59.3	6.04	0.46	0.058**	0.008**
	3	2	12	34.3	77.2	1.11	0.09	0.906	0.664

[†] **Rayleigh's Test of Uniformity (R-Test):** Assesses if orientation significantly deviated from a random distribution (i.e., a general unimodal distribution with unknown mean direction and vector length).

[‡] **V-Test (Alternative with Specified Mean Direction):** Assesses if orientation significantly deviated from a unimodal distribution with specified mean direction. We hypothesized that animals would move toward nearest forest edge(s): 270° at Trans 1; either 180° (1) or 270° (2) at Trans 2; and 180° at Trans 3.

Table 3.2. (continued)

Notes: The first six rows combine all replicates along entire transects (30^0 , 45^0 , and 60^0). Distance classes comprise two categories of frog release locations along transects measured in meters from forest corner (Class 1: 8, 20, 32, and 44 m; Class 2: 56, 68, and 80 m). Circular statistics were used to test if frogs significantly oriented movements toward the bearing of the nearest forest edge(s): Transect 1: 270^0 ; Transect 2: equidistant to 180^0 and 270^0 ; Transect 3: 180^0). Statistics included: mean direction (i.e., average azimuth of resultant vector); vector magnitude (i.e., r , or length of the mean vector); and consistency ratio (% of normalized magnitude of the resultant vector ranging from 0-1; larger r values indicate that observations were clustered more closely around the mean). Data included $n = 157$ frogs (of 168) that moved > 0.1 m. Statistical tests were deemed significant at $P \leq 0.05$ (**); marginal significance is indicated at $P \leq 0.08$ (*).

Discussion

To predict functional connectivity for species in fragmented landscapes, many researchers reject the traditional views of the matrix as homogeneously inhospitable (Revilla et al., 2004; Eycott et al., 2012), and instead recognize that it may comprise a continuum of conditions that tend to filter or facilitate movement (Kuefler et al., 2010). If matrix vegetation influences the probability of entry and transit success, then how the matrix is managed may shape dispersal and many conservation outcomes (Driscoll et al., 2013). We studied the movement of juvenile *L. sylvaticus* released in different open-cover types and determined that matrix condition affects behavior. Prior studies have quantified either the overall permeability of open-canopy cover types to juvenile movements (e.g., Rothermel and Semlitsch, 2002; Cline and Hunter, 2014) or fine-scale locomotor ability on different substrates (e.g., Stevens et al., 2004; Baughman and Todd, 2007). Our study bridges this previous work to provide direct estimates of fine-scale movement once matrix edges are crossed and in relation to landscape configuration. In treatments with lower structural complexity, juveniles adopted straighter paths, exhibited greater overall scales and rates of movement, and oriented toward forested cover types from distances as great as 40-55 m (asphalt > lawn > corn > forest > hay; Figures 3.2 and 3.3). This finding indicates that these are different ecological filters to juvenile movements, and therefore it may be overly simplistic and inaccurate to assume movement performance is uniform across all matrix types.

Substrate structure and locomotion

Juveniles moved differently across different substrate types. As predicted, hay constituted the greatest physical filter, while asphalt and grass permitted faster movement (Figure 3.2D), greater overall displacement (Figure 3.2A), and straighter trajectories (Figure 3.2C) toward suitable habitat. Metamorphs in the forest and corn demonstrated similar and consistently moderate movement patterns for all five metrics, which could suggest that some level of overhead cover may mitigate microclimate (Figure 3.4) and decrease perceived predation risk. Previous studies have demonstrated that locomotor ability depends on the surface crossed (e.g., Eycott et al., 2012), but results vary. Juveniles of three species differed in their response to old-field matrix and forest, with two species (*Anaxyrus americanus* and *Ambystoma maculatum*) moving greater distances with higher survival in the forest (Rothermel and Semlitsch, 2002). In a laboratory study of natterjack toads (*Epidalea calamita*), the vertical structure of substrates inhibited hopping (grass, field, and forest), while sand and cement increased the length and speed of moves (Stevens et al., 2004). Researchers also found that movements of southern graycheek salamanders (*Plethodon metcalfi*) were greater in substrates with less structural complexity (lawn, gravel, asphalt compared to leaf litter and bare soil: Semlitsch et al., 2012). Taken together, these results support the hypothesis that simplified vegetation structure represents low impedance, but there may be other factors (e.g., desiccation and predation risk) that influence movement performance. For example, a recent study of juvenile amphibian movement in agroecosystems found that water loss was greater in corn and soybean fields compared to forest or prairie, thus suggesting resistance costs of movement due to desiccation may not be uniform in all

agricultural settings (Consentino et al., 2011). However, we found little evidence that frog weight or SVL were correlated with movement metrics. Thus, it was unlikely that larger frogs in our study perceived lower desiccation risk than small individuals on substrates like asphalt or lawn where temperature and humidity fluctuated most (Figure 3.4; Peterman et al., 2013).

Latency not predicted by substrates or single factors

Prior to our experiments, we predicted that latency would be longer in substrates with greater “settling” habitat (forest) and physical cover (hay, corn) assuming that frogs perceived these as a refuge from thermal stress or predators. In actuality, we observed high variation within treatments, and could not predict latency based on substrate types. Among treatments, the average latency was longest in the lawn and asphalt (208 ± 50 s and 173 ± 51 s, respectively), intermediate in the corn (123 ± 61 s), and shortest in the hay and forest (94 ± 31 s and 61 ± 13 s, respectively) although, the high within-treatment, but low between-treatment variability (Figure 3.2B) made this pattern statistically insignificant and difficult to interpret. In contrast to our prediction, results suggest that open substrates could present greater perceived predation risk, causing frogs to crouch and cease motion in response to lack of cover. Indeed, our other metrics showcase the ability of frogs to evacuate quickly over long distances in lawn and asphalt, moving toward forest (Figure 3.3). Recent studies have quantified substantial predation risks to juveniles during initial movement from ponds; e.g., 23% of ringed salamanders (*A. annulatum*) were consumed by predators during their first night in terrestrial habitat (Pittman et al., 2013b). Although we need more information (e.g., predator abundance),

our latency results suggest that predation alone is not driving patterns of substrate-specific movement (e.g., Lillywhite and Brishcoux, 2011). For frogs deciding when to make initial movements, we posit that they were responding to an interplay of ecological pressures that reach beyond the microclimate and predation factors discussed above (e.g., to include food availability: Nieceza, 2000; density-dependent behavior: Patrick et al., 2008; or physiological stress: Janin et al., 2012b).

Distance to forest-edge and orientation

Our directionality data suggest that juveniles ranging through non-forested matrix may be able to locate settling habitat at scales that are relevant to landscape configuration. Specifically, we determined that juveniles were able to orient toward the nearest forest 35-40 m away when released in asphalt, lawn, or corn, but not hay (Figure 3.3 and Appendix E). This pattern was corroborated in our second experiment with greater directionality toward forest in lawn (Figure 3.5A) than in hay (Figure 3.5B). These findings are consistent with: (1) the “evacuation” hypothesis (Semlitsch et al., 2008), which suggests that individuals evade inhospitable conditions in open vegetation; and (2) our prediction that forest-targeted directionality would be greatest in treatments with lower structural complexity. Prior studies have demonstrated that vegetation structure and surrounding landscape configuration may affect juvenile orientation (Walston and Mullin, 2008); for example, juvenile spotted salamanders (*A. maculatum*) exhibited greater forest-targeted orientation in field versus early-successional vegetation (Pittman and Semlitsch, 2013a). Similarly, Rothermel and Semlitsch (2002) found that juvenile American toads (but not small-mouthed salamanders, or adults of either species)

in old-fields moved toward forest (*Bufo americanus* and *A. texanum*, respectively). Such results suggest that species-specific studies are necessary and that juveniles and adults may employ different movement mechanisms.

There may also be distance thresholds at which individuals no longer orient to forest due to decreased perceptual range. Frogs in lawns tended to exhibit forest directionality at greater distances compared to hayfields (i.e., up to 44-56 m and nearly significant at distances extending to 80 m; Appendix EA). Amphibians have been shown to rely on a diversity of orientation mechanisms including, but not limited, to olfaction (Popescu et al., 2012b), visual cues or light polarization (Dall'Antonia and Sinsch, 2001; Phillips et al., 2010), acoustic cues (Bee, 2013), and magnetic reception (Landler and Gollmann, 2011), although we were unable to test these mechanisms. In addition, there may be compounding factors that we were unable to measure, such as the locomotive costs of moving through dense hay. Metamorphs may balance the costs of long-distance movement decisions against assessing local resources for food and cover, and it is possible that frogs in hayfields sought temporary refuge rather than attempt a single long-distance movement to forest edge overnight (*see* Cline and Hunter, 2014). From our observations in forest, we know that frogs in suitable habitat will move at random (Figure 3.3) and initially only at moderate distances ($\sim 9.44 \pm 2.11$ mean path length) and velocities (Table 3.1, Figure 3.2). Results support the notion that some open-cover types may afford temporary settling habitat ("retreat" hypothesis; Semlitsch et al., 2008) and that juveniles did not immediately move toward forest. This line of reasoning suggests that our hayfield orientation results may not be meaningful if frogs adopted a settling strategy at least initially.

Potential influence of microclimate on movements: Nocturnal refugia in the matrix

It is well established that microclimate influences the physiological ecology of amphibians, and juveniles may be particularly vulnerable to desiccation risk in open cover due to their small size and increased surface area to volume ratios (Lillywhite, 1970; Rittenhouse et al., 2008). Our microclimate data (Figure 3.4) suggest that nocturnal regimes were mild and moist enough in all five substrates to allow successful transit. However, average daytime values consistently peaked at $> 30\text{-}35^{\circ}\text{C}$ and $< 45\text{-}50\%$ at refugia in the asphalt and lawn, suggesting that physiological stress would be greatly increased for a frog by day and could represent an ecological trap. This was in stark contrast to patterns in the corn, forest, and hay, where humidity was consistently between 80-95% and daily temperature fluctuated least ($16\text{-}30^{\circ}\text{C}$). Our observed high temperatures and dry microclimates in the asphalt and grass (Figure 3.4) are consistent with our prediction that frogs would exhibit the straightest paths and greatest velocities to evacuate substrates with the most thermoregulatory risk.

Future studies and management implications

To predict amphibian population connectivity in fragmented landscapes we need to better integrate field-based measurements of individual movements in a diversity of matrix types with data on how movement is influenced by landscape configuration (Bélisle, 2005, Driscoll et al., 2013). Both types of information are necessary for parameterizing individual-based models of dispersal (e.g., Nathan et al., 2002; Hudgens et al., 2012). This study provides direct measures of fine-scale movements of a critical life stage (dispersing juveniles; Pittman et al., 2014) in five vegetation types, and

quantifies orientation to the nearest forest. Paired with prior estimates of frog willingness to enter the non-forest matrix (i.e., the degree to which matrix type either impedes or facilitates frog entry from a forest edge; Cline and Hunter, 2014), our results could provide the basis for predicting how the composition and configuration of the matrix might be managed to reduce the effective isolation of habitat patches. Our distinctions among non-forest matrix types are important because many landscape population models use expert-based values that are a one-size-fits-all measure for open cover (Yackulic et al., 2011).

We have demonstrated that open-canopy cover types may differ as filters or conduits to juvenile movements, and this fills a critical gap in our understanding of the behavioral mechanisms that underpin the relationship between matrix structure and the distribution of a patch-dependent species. These distinctions may inform land-use planning; for example, how the composition and configuration of these cover types should be integrated with forest distribution to reduce the “effective” isolation of (and not just Euclidean distance between) patches of preferred habitats for dispersing amphibians. Our tracking design provides a minimally invasive way to record fine-scale directed movement behavior, but a more complete understanding of dispersal requires long-term monitoring of individual fitness and behavior. This will require new technology for direct tracking of small animals over long periods. Additionally, our study only provides a limited assessment of the processes that could shape juvenile movements. For example, we also need to assess how seasonal land management practices such as crop-rotation, thinning, harvest, mowing, pesticide application can be best designed (including distribution in time and space) to facilitate dispersal. Research on the mechanisms that

influence ranging behavior over multiple seasons and longer time scales will provide a better understanding of when juveniles switch between movement modes (i.e., away, directed, and settlement; Pittman et al., 2014), and thus how juvenile dispersal can be facilitated to maintain functional connectivity in fragmented landscapes.

REFERENCES

- Arseneault, J.E., M.R. Saunders, R.S. Seymour, and R.G. Wagner. 2011. First decadal response to treatment in a disturbance-based silviculture experiment in Maine. *Forest Ecology and Management* 262:404-412.
- Baker, S.C., T.A. Spies, T.J. Wardlaw, J. Balmer, J.F. Franklin, and G.J. Jordan. 2013. The harvested side of edges: Effect of retained forests on the re-establishment of biodiversity in adjacent harvested areas. *Forest Ecology and Management* 302:107-121.
- Baldwin, R.F., A.J.K. Calhoun, and P.G. deMaynadier. 2006. Conservation planning for amphibian species with complex habitat requirements: A case study using movements and habitat selection of the wood frog *Rana sylvatica*. *Journal of Herpetology* 40:442-453.
- Barbasch, T., and M.F. Benard. 2011. Past and present risk: Exposure to predator chemical cues before and after metamorphosis influences juvenile wood frog behavior. *Ethology* 117:367-373.
- Barraquand, F., and S. Benhamou. 2008. Animal movements in heterogeneous landscapes: identifying profitable places and homogeneous movement bouts. *Ecology* 89:3336-3348.
- Bartoń, K.A., B.L. Phillips, J.M. Morales, and J.M.J. Travis. 2009. The evolution of an 'intelligent' dispersal strategy: biased, correlated random walks in patch landscapes. *Oikos* 118:309-319.
- Bataineh, M., L. Kenefic, A. Weiskittel, R. Wagner, and J. Brissette. 2013. Influence of partial harvesting and site factors on the abundance and composition of natural regeneration in the Acadian Forest of Maine, USA. *Forest Ecology and Management* 306:96-106.
- Bates, D., M. Maechler, and B. Bolker, B. 2011. lme4: Linear mixed-effects models using s4 classes. < <http://lme4.r-forge.r-project.org/>>

- Baughman, B., and B.D. Todd. 2007. Role of substrate cues in habitat selection by recently metamorphosed *Bufo terrestris* and *Scaphiopus holbrookii*. *Journal of Herpetology* 41:154-157.
- Bee, M.A. 2013. Sound source perception in anuran amphibians. *Current Opinion in Neurobiology* 22:301-310.
- Bélisle, M. 2005. Measuring landscape connectivity: The challenge of behavioral landscape ecology. *Ecology* 86:1988-1995.
- Berven, K. A., and T.A. Grudzien. 1990. Dispersal in the wood frog (*Rana sylvatica*): implications for genetic population structure. *Evolution* 44:2047-2056.
- Bolker, B. M., M.E. Brooks, C.J. Clark, S.W. Geange, J.R. Poulsen, M.H.H. Stevens, and J.S.S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution* 24:127-135.
- Brissette, J.C. 1996. Effects of intensity and frequency of harvesting on abundance and composition of natural regeneration in the Acadian Forest of eastern North America. *Silva Fennica* 30:301-314.
- Burgess, S.C., E.A. Treml, and D.J. Marshall. 2012. How do dispersal costs and habitat selection influence realized population connectivity? *Ecology* 96:1378-1387.
- Calhoun, A.J.K., and P. deMaynadier. 2004. Forestry Habitat Management Guidelines for Vernal Pool Wildlife. MCA Technical Paper No. 6, Metropolitan Conservation Alliance, Wildlife Conservation Society, New York.
- Calhoun, A.J.K., N.A. Miller, and M.W. Klemens. 2005. Conserving pool-breeding amphibians in human-dominated landscapes through local implementation of Best Development Practices. *Wetlands Ecology and Management* 13:291-304.
- Cline, B.B., and M.L. Hunter, Jr. Movement in the matrix: Substrates and distance to forest edge affect amphibian dispersal. *Ecological Applications*. *In review*.

- Cline, B.B., and M.L. Hunter, Jr. Heavy partial harvests and the initial movements of a dispersing forest amphibian in the Acadian forest of Maine, USA. *Forest Ecology and Management. In review.*
- Cline, B.B., and M.L. Hunter, Jr. 2014. Different open-canopy vegetation types affect matrix permeability for a dispersing forest amphibian. *Journal of Applied Ecology* 51:319-329.
- Clobert, J., J. LeGalliard, J. Cote, S. Meylan, and M. Massot. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecology Letters* 12: 197-209.
- Cosentino, B.J., R.L. Schooley, and C.A. Phillips. 2011. Connectivity of agroecosystems: Dispersal costs can vary among crops. *Landscape Ecology* 26:371-379.
- Cushman, S.A. 2006. Effects of habitat loss and fragmentation on amphibians: A review and prospectus. *Biological Conservation* 128:231-240.
- Dall'Antonia, P., and U. Sinsch. 2001. In search of water: orientation behavior of dehydrated natterjack toads, *Bufo calamita*. *Animal Behaviour* 61:617-629.
- deMaynadier, P.G., and M.L. Hunter, Jr. 1995. The relationship between forest management and amphibian ecology: A review of the North American literature. *Environmental Reviews* 3:230-261.
- deMaynadier, P.G., and M.L. Hunter, Jr. 1998. Effects of silvicultural edges on the distribution and abundance of amphibians in Maine. *Conservation Biology*, 12, 340-352.
- deMaynadier, P.G., and M.L. Hunter, Jr. 1999. Forest canopy closure and juvenile emigration by pool-breeding amphibians in Maine. *Journal of Wildlife Management* 63: 441-450.
- Desrochers, R.E., J.T. Kerr, and D.J. Currie. 2011. How, and how much, natural cover loss increases species richness? *Global Ecology and Biogeography* 20:857-867.

- Dingle, H. 1996. *Migration: The Biology of Life on the Move*. Oxford University Press, USA.
- Driscoll, D.A., S.C. Banks, P.S. Barton, D.B. Lindenmayer, and A.L. Smith. 2013. Conceptual domain of the matrix in fragmented landscapes. *Trends in Ecology and Evolution* 28:605-613.
- Eggert, C. 2002. Use of fluorescent pigments and implantable transmitters to track a fossorial toad (*Pelobates fuscus*). *Herpetological Journal* 12:69-74.
- Eycott, A.E., G.B. Stewart, L.M. Buyyng-Ali, D.E. Bowler, K. Watts, K. and A.S. Pullin. 2012. A meta-analysis on the impact of different matrix structures on species movement rates. *Landscape Ecology*, 27, 1263-1278.
- Feder, M.E. 1983. Integrating the ecology and physiology of Plethodontid salamanders. *Herpetologica* 39:291-310.
- Fisher, N.I. 1993. *Statistical Analysis of Circular Data*. Cambridge University Press, Cambridge, UK.
- Forman, R.T.T. 1995. *Land Mosaics*. Cambridge University Press, Cambridge, UK.
- Fox, J., and S. Weisberg. 2011. *An R Companion to Applied Regression*, 2nd edn., Sage, Blackwood Oaks, California <<http://CRAN.R-project.org/package=car>>.
- Fraver, S., A.S. White, and R.S. Seymour. 2009. Patterns of natural disturbance in an old-growth landscape of northern Maine, USA. *Journal of Ecology* 97:289–298.
- Fuller, A.K., D.J. Harrison, and H.J. Lachowski. 2004. Stand-scale effects of partial harvesting and clearcutting on small mammals and forest structure. *Forest Ecology and Management* 191:373-386.
- Graham-Sauvé, L., T.M. Work, D. Kneeshaw, and C. Messier. 2013. Shelterwood and multicohort management have similar initial effects on ground beetle assemblages in boreal forests. *Forest Ecology and Management* 306:266-274.

- Harper, K.A., S.E. Macdonald, P.J. Burton, J. Chen, K. Brososke, S. Saunders, E. Euskirchen, D. Roberts, M. Jaiteh, and P.A. Esseen. 2005. Towards a theory of edge influence: Forest structure and composition at created edges. *Conservation Biology* 19:768-782.
- Harper, C.A., and D.C. Gwynn Jr. 1999. Factors affecting salamander density and distribution within four forest types in the Southern Appalachian Mountains. *Forest Ecology and Management* 114:245-252.
- Harpole, D.N., and C.A. Haas. 1999. Effects of seven silvicultural treatments on terrestrial salamanders. *Forest Ecology and Management* 114:349-356.
- Haynes, K.J., and J.T. Cronin. 2006. Interpatch movement and edge effects: the role of behavioral responses to the landscape matrix. *Oikos* 113:43-54.
- Hocking, D.J., G.M. Connette, C.A. Conner, B.R. Scheffers, S.E. Pittman, W.E. Peterman, and R.D. Semlitsch. 2013. Effects of experimental forest management on a terrestrial, woodland salamander in Missouri. *Forest Ecology and Management* 287:32-39.
- Homyack, J.A., and C.A. Haas. 2009. Long-term effects of silvicultural forest harvesting on abundance and reproductive demography of terrestrial salamanders. *Biological Conservation* 142:110-121.
- Homyack, J.A., and C.A. Haas. 2013. Effects of repeated stand entries on terrestrial salamanders and their habitat. *Southeastern Naturalist* 12:353-366.
- Hothorn, T., K. Hornik, M.A. van de Wiel, and A. Zeileis. 2008. Implementing a class of permutation tests: The coin package. *Journal of Statistical Software* 28:1-23.
- Hudgens, B.R., W.F. Morris, N.M. Haddad, W.R. Fields, J.W. Wilson, D. Kuefler, and T. Jobe. 2012. How complex do models need to be to predict dispersal of threatened species through matrix habitats? *Ecological Applications* 22:1701-1710.
- Hunter, M.L, Jr., and F. Schmiegelow. 2011. *Wildlife, Forests, and Forestry: Principles of Managing Forests for Biological Diversity*, second ed. Prentice-Hall, New Jersey.

- Jammalamadaka, S.R., and A. SenGupta. 2001. Topics in Circular Statistics. World Scientific Publishing, Singapore.
- Janin, A., J-P Léna, and P. Joly. 2012a. Habitat fragmentation affects movement behavior of migrating juvenile common toads. *Behavioral Ecology and Sociobiology* 66:1351-1356.
- Janin, A., J-P. Léna, S. Deblois, and P. Joly. 2012b. Use of stress-hormone levels and habitat selection to assess functional connectivity of a landscape for an amphibian. *Conservation Biology* 26:923-931.
- Karraker, N.E., and H.H. Welsh, Jr. 2006. Long-term impacts of even-aged timber management on abundance and body condition of terrestrial amphibians in Northwestern California. *Biological Conservation* 131:132-140.
- Kuefler, D., B. Hudgens, N.M. Haddad, W.F. Morris, and N. Thurgate. 2010. The conflicting role of matrix habitats as conduits and barriers for dispersal. *Ecology* 91:944-950.
- Kupfer, J.A., G.P. Malanson, and S.B. Franklin. 2006. Not seeing the ocean for the islands: the mediating influence of matrix-based processes on forest fragmentation effects. *Global Ecology and Biogeography* 15:8-10.
- Landler, L., and G. Gollmann. 2011. Magnetic orientation of the Common Toad: establishing an arena approach for adult anurans. *Frontiers in Zoology* 8:6 <doi:10.1186/1742-9994-8-6>
- Lillywhite, H.B. 1970. Behavioral temperature regulation in the bullfrog, *Rana catesbeiana*. *Copeia* 1970:158-168.
- Lillywhite, H.B., and F. Brischoux. 2012. Is it better in the moonlight? Nocturnal levels of insular cottonmouth snakes increases with lunar light levels. *Journal of Zoology* 286:194-199.

- Lindstrom, J.C., and D.M. Bates. 1990. Nonlinear mixed effects models for repeated measures data. *Biometrics* 46:673-687.
- Lund, U., and C. Agostinelli. 2013. Circular Statistics, An R Package: 'circular,' Vers. 0.4-7. <<http://CRAN.R-project.org/package=circular>>.
- Maine Forest Service, 2013. 2012 Silvicultural Activities Report, including Annual Report on Clearcutting and Precommercial Activities. Department of Agriculture, Conservation, and Forestry, Augusta, Maine, USA.
- McDonough, C., and P.W.C. Paton. 2006. Salamander dispersal across a forested landscape fragmented by a golf course. *Journal of Wildlife Management* 71:1163-1169.
- Morneault, A.E., B.J. Naylor, L.S. Schaeffer, and D.C. Othmer. 2004. The effect of shelterwood harvesting and site preparation on eastern red-backed salamanders in white pine stands. *Forest Ecology and Management* 199:1-10.
- Nams, V.O. 2011. Emergent properties of patch shapes affect edge permeability to animals. *PLoS ONE*. 6:e21886.
- Nathan, R., G.G. Katul, H.S. Hoen, S.M. Thomas, R. Oren, R. Avissar, S.W. Pacala, and S.A. Levin. 2002. Mechanisms of long-distance dispersal of seeds by wind. *Nature* 418:409-413.
- Nicieza, A.G. 2000. Interacting effects of predation risk and food availability on larval anuran behavior and development. *Oecologia*. 123:497-505.
- Olson, M.G., and R.G. Wagner. 2010. Long-term compositional dynamics of Acadian mixedwood stands under different silvicultural regimes. *Canadian Journal of Forest Research* 40:1993-2002.
- Patrick, D.A., E.B. Harper, M.L. Hunter, Jr., and A.J.K. Calhoun, A.J.K. 2008. Terrestrial habitat selection and strong density-dependent mortality in recently metamorphosed amphibians. *Ecology* 89:2563-2574.

- Peel, M.C., B.L. Finlayson, and T.A. McMahon. 2007. Updated world map of the Köppen Geiger climate classification. *Hydrology and Earth System Sciences* 11:1633-1644.
- Perkins, D.W., and M.L. Hunter, Jr. 2006. Effects of riparian timber management on amphibians in Maine. *Journal of Wildlife Management* 70:657-670.
- Peterman, W.E., J.L. Locke, and R.D. Semlitsch. 2013. Spatial and temporal patterns of water loss in heterogeneous landscapes: Using plaster models as amphibian analogues. *Canadian Journal of Zoology* 91:135-140.
- Petranka, J.W., M.E. Eldridge, and K.E. Haley. 1993. Effects of timber harvesting on southern Appalachian salamanders. *Conservation Biology* 7:363-370.
- Phillips, J.B., P.E. Jorge, and R. Muheim. 2010. Light-dependent magnetic compass orientation in amphibians and insects: candidate receptors and candidate molecular mechanisms. *Journal of the Royal Society Interface*. <doi:10.1098/rsif.2009.0459.focus>
- Pinheiro, J.C., and D.M. Bates. 2000. *Mixed Effects Models in S and S-Plus*, Springer, New York.
- Pittman, S.E., M.S. Osbourn, and R.D. Semlitsch. 2014. Movement ecology of amphibians: A missing component for understanding population declines. *Biological Conservation* 169:44-53.
- Pittman, S.E., and R.D. Semlitsch, R.D. 2013a. Habitat type and distance to edge affect movement behavior of juvenile pond-breeding salamanders. *Journal of Zoology* 291:154-162.
- Pittman, S.E., M.S. Osbourn, D.L. Drake, and R.D. Semlitsch. 2013b. Predation of juvenile ringed salamanders (*Ambystoma annulatum*) during initial movement out of ponds. *Herpetological Conservation and Biology* 8:681-687.
- Popescu, V.D., and Hunter, Jr., M.L. 2011. Clearcutting affects habitat connectivity for a forest amphibian by decreasing permeability to juvenile movements. *Ecological Applications* 21:1283-1295.

- Popescu, V.D., D.A. Patrick, and M.L. Hunter, M.L., Jr. 2012a. The role of forest harvesting and subsequent vegetative regrowth in determining patterns of amphibian habitat use. *Forest Ecology and Management* 270:163-174.
- Popescu, V.D., B.S. Brodie, M.L. Hunter, Jr., and J.D. Zydlweski. 2012b. Use of olfactory cues by newly metamorphosed wood frogs (*Lithobates sylvaticus*) during emigration. *Copeia* 3:424-431.
- Prevedello, J.A., and M.V. Vieira. 2010. Does the type of matrix matter? A quantitative review of the evidence. *Biodiversity Conservation* 19:1205-1223.
- Reichenbach, N., and P. Sattler. 2007. Effects of timbering on *Plethodon hubrichti* over twelve years. *Journal of Herpetology* 41:622-629.
- Revilla, E., T. Wiegand, F. Palomares, P. Ferreras, and M. Delibes. 2004. Effects of matrix heterogeneity on animal dispersal: From individual behavior to metapopulation level parameters. *The American Naturalist* 164:E130-E153.
- Rittenhouse, T.A.G., and R.D. Semlitsch. 2006. Grasslands as movement barriers for a forest-associated salamander: Migration behavior of adult and juvenile salamanders at a distinct habitat edge. *Biological Conservation* 131:14-22.
- Rittenhouse, T.A.G., T.T. Althether, and R.D. Semlitsch. 2006. Fluorescent powder pigments as a harmless tracking method for ambystomatids and ranids. *Herpetological Review* 37:188-191.
- Rittenhouse, T.A.G., E.B. Harper, L.R. Rehard, and R.D. Semlitsch, R.D. 2008. The role of microhabitats in the dessication and survival of anurans in recently harvested oak hickory forest. *Copeia* 4:807-814.
- Rohr, J.R., T.R. Raffel, N.T. Halstead, T.A. McMahon, S.A. Johnson, R.K. Boughton, and L.B. Martin. 2013. Early-life exposure to an herbicide has enduring effects on pathogen-induced mortality. *Proceedings of the Royal Society of Biology* 280:1772.

- Rosenvald, R., and A. Lõhmus. 2008. For what, when, and where is green-tree retention better than clear-cutting? A review of the biodiversity aspects. *Forest Ecology and Management* 255:1-15.
- Rothermel, B.B., and R.D. Semlitsch. 2002. An experimental investigation of landscape resistance of forest versus old-field habitats to emigrating juvenile amphibians. *Conservation Biology* 16:1324-1332.
- Sader, S.A., M. Bertrand, and E.H. Wilson. 2003. Satellite change detection of forest harvest patterns on an industrial forest landscape. *Forest Science* 49:341-353.
- Saunders, M., and R. Wagner. 2008. Long-term spatial and structural dynamics in Acadian mixedwood stands managed under various silvicultural systems. *Canadian Journal of Forest Research* 38:498-517.
- Scheffers, B.R., B.L.S. Furman, and J.P. Evans. 2013. Salamanders continue to breed in ephemeral ponds following the removal of surrounding terrestrial habitat. *Herpetological Conservation and Biology* 8:715-723.
- Schtickzelle, N., and M. Baguette. 2003. Behavioural responses to habitat patch boundaries restrict dispersal and generate emigration-patch area relationships in fragmented landscapes. *Journal of Animal Ecology* 72:533-545.
- Semlitsch, R.D. 2008. Differentiating migration and dispersal processes for pond breeding amphibians. *Journal of Wildlife Management* 72:260-267.
- Semlitsch, R.D., and J.R. Bodie. 2003. Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. *Conservation Biology* 17:1219-1220.
- Semlitsch, R.D., C.A. Connor, D.J. Hocking, T.A.G. Rittenhouse, and E.B. Harper. 2008. Effects of timber harvesting on pond-breeding amphibian persistence: Testing the evacuation hypothesis. *Ecological Applications* 18:283-289.

- Semlitsch, R.D., B.D. Todd, S.M. Blomquist, A.J.K. Calhoun, J.W. Gibbons, J.P. Gibbs, G.J. Graeter, E.B. Harper, D.J. Hocking, M.L. Hunter Jr., D.A. Patrick, T.A.G. Rittenhouse, and B.B. Rothermel. 2009. Effects of timber harvest on amphibian populations: understanding mechanisms from forest experiments. *BioScience* 59:853-862.
- Semlitsch, R.D., S. Ecrement, A. Fuller, K. Hammer, J. Howard, C. Krager, J. Mozeley, J. Ogle, N. Shipman, J. Speier, M. Walker, and B. Walters. 2012. Natural and anthropogenic substrates affect movement behavior of the Southern Graycheek Salamander (*Plethodon metcalfi*). *Canadian Journal of Zoology* 90:1128-1135.
- Seymour, R. S. 1995. The Northeastern Region, in: Barrett, J.W., (Ed.), *Regional Silviculture of the United States*, third ed. Wiley and Sons, New York, pp. 31-79.
- Seymour, R.S., A.S. White, and P.G. deMaynadier. 2002. Natural disturbance regimes in northeastern North America – evaluating silvicultural systems using natural scales and frequencies. *Forest Ecology and Management* 155:357-367.
- Stamps, J.A., M. Buechner, and V.V. Krishnan. 1987. The effects of edge permeability and habitat geometry on emigration from patches of habitat. *American Naturalist* 129:533-552.
- Stevens, V.M., E. Polus, R.A. Wesselingh, N. Schtickzelle, and M. Baguette. 2004. Quantifying functional connectivity: experimental evidence for patch-specific resistance in the Natterjack Toad (*Bufo calamita*). *Landscape Ecology* 19:829-842.
- Steventon, J.D., K.L. MacKenzie, and T.E. Mahon. 1998. Response of small mammals and birds to partial cutting and clearcutting in northwest British Columbia. *Forestry Chronicles* 74:703-713.
- Thorpe, H., and S. Thomas. 2007. Partial harvesting in the Canadian boreal: Success will depend on stand dynamic responses. *Forestry Chronicles* 83:319-325.
- Tilghman, J.M., S.W. Ramee, and D.M. Marsh. 2012. Meta-analysis of the effects of canopy removal on terrestrial salamander populations in North America. *Biological Conservation* 152:1-9.

- Todd, B.D., S.M. Blomquist, E.B. Harper, and M.S. Osbourn. 2014. Effects of timber harvesting on terrestrial survival of pond-breeding amphibians. *Forest Ecology and Management* 313:123-131.
- Turchin, P. 1998. *Quantitative Analysis of Movement: Measuring and Modeling Population Redistribution in Animals and Plants*. Sinauer Associates, Inc., Sunderland, Massachusetts, USA.
- Turner, M.G., D.C. Donato, and W.H. Romme. 2013. Consequences of spatial heterogeneity for ecosystem services in changing forest landscapes: Priorities for future research. *Landscape Ecology* 28:1081-1097.
- Van Buskirk, J. 2012. Permeability of the landscape matrix between amphibian breeding sites. *Ecology and Evolution* 2:3160-3167.
- Vanderwel, M.C., S.C. Mills, and J.R. Malcolm. 2009. Effects of partial harvesting on vertebrate species associated with late-successional forests in Ontario's boreal region. *Forestry Chronicles* 85: 91-104.
- Vanderwel, M.C., J.P. Caspersen, J.R. Malcolm, M.J. Papaik, and C. Messier. 2011. Structural changes and potential vertebrate responses following simulated partial harvesting of boreal mixedwood stands. *Forest Ecology and Management* 261:1362-1371.
- Vasconcelos, D., and A.J.K. Calhoun. 2004. Movement patterns of adult and juvenile *Rana sylvatica* (LeConte) and *Ambystoma maculatum* (Shaw) in three restored seasonal pools in Maine. *Journal of Herpetology* 38:551-561.
- Vos, C.C., P.W. Goedhart, D.R. Lammertsma, and A.M. Spitzen-Van der Sluijs. 2007. Matrix permeability of agricultural landscapes: an analysis of movements of the common frog (*Rana temporaria*). *Herpetological Journal* 17:174-182.
- Walston, L.J., and S.J. Mullin. 2008. Variation in amount of surrounding forest habitat influences the initial orientation of juvenile amphibians emigrating from breeding ponds. *Canadian Journal of Zoology* 86:141-146.

- Walton, B.M. 2005. Salamanders in forest-floor food webs: Environmental heterogeneity affects the strength of top-down effects. *Pedobiologia* 49:51-60.
- Yackulic, C.B., S. Blake, S. Deem, M. Kock, and M. Uriarte. 2011. One size does not fit all: flexible models are required to understand animal movement across scales. *Journal of Animal Ecology* 80:1088-1096.
- Zeller, K.A., K. McGarigal, and A.R. Whiteley. 2012. Estimating landscape resistance to movement: a review. *Landscape Ecology* 27:777-797.

APPENDICES

APPENDIX A: OBSERVED AND PREDICTED PROPORTIONS OF RELEASED JUVENILE *LITHOBATES SYLVATICUS* REACHING 10-, 20-, AND 30-M DISTANCES IN FIVE OPEN CANOPY-COVER TREATMENTS

Observed and predicted proportions of released juvenile *Lithobates sylvaticus* reaching 10-, 20-, and 30-m distances (from perpendicular interface with forest edge) in five open canopy-cover treatments in 2010, and 2 reference treatments (forest clearcut and mature forest) in 2008-09 (see Appendix 1; A021-059-A1 in Popescu and Hunter, 2011). Forest clearcut treatments comprise the same experimental runways across both studies (2008-10). GLMEs include both fixed effects (sources of experimental variance) and random effects (variance from experimental units selected at random, Bolker et al., 2009), and are widely used to treat non-normal data. We inspected GLME model deviance, and found no evidence of block random effects for models with variables *treatment* and *runway* as fixed effects, and *batch* as a random effect (program R version 2.13.2, package [lme4]; Bates et al., 2011). Thus, we generated predictions using generalized linear models (GLM), using a quasi-binomial distribution for proportions (logit canonical-link function). We ran simple models followed by the first-order interaction of *treatment* x *runway*, due to (1) ambiguity interpreting coefficients of complex models; and (2) relatively low sample sizes (i.e., 147 tracks and 349 captures out of 561 released). We assessed model fit using plots of (1) quantile-quantile; (2) constant leverage; and (3) predicted vs. observed values. We fit final models by inspecting overdispersion and *F*-tests (ANOVA) for model comparison. Among all distances, simplified models had

greatest support. Interaction terms (*treatment* x *runway*) were not significant, suggesting no differences in the number of tracks among runways (n=2) within treatments. Our GLMs for 10- and 30-m included *treatment*; it was only at 20-m where we found additive effects (*treatment* + *runway*).

Table A.1 Observed and predicted proportions of released juvenile *L. sylvaticus* reaching 10-, 20-, and 30-m distances in five open canopy-cover treatments in 2010, and 2 reference treatments (forest clearcut and mature forest) in 2008-09.

Distance from edge (m)	Treatment (2010)						Reference Treatment (2008-09)	
		Clearcut	Hayfield	Row crop (corn)	Lawn (0% cover)	Lawn (45-85% cover)	Clearcut	Mature forest
10 - m	<i>Mean</i> \pm <i>SE</i> *	0.15 \pm 0.03	0.05 \pm 0.02	0.18 \pm 0.04	0.11 \pm 0.03	0.20 \pm 0.04	0.31 \pm 0.06	0.67 \pm 0.06
	<i>Coefficient</i> \pm <i>SE</i> **	-1.653 \pm 0.271	-1.128 \pm 0.504	0.118 \pm 0.376	-0.385 \pm 0.413	0.226 \pm 0.370	0.877 \pm 0.215	0.628 \pm 0.212
	<i>Predicted</i> 95% <i>CI</i> ***	(-2.220, 1.150)	(-2.198, -0.188)	(-0.621, 0.864)	(-1.216, 0.419)	(-0.499, 0.962)	(-1.300, -0.454)	(0.212, 1.045)
20 - m	<i>Mean</i> \pm <i>SE</i> *	0.08 \pm 0.03	0.03 \pm 0.01	0.11 \pm 0.03	0.08 \pm 0.03	0.13 \pm 0.03	0.23 \pm 0.05	0.61 \pm 0.08
	<i>Coefficient</i> \pm <i>SE</i> **	-2.442 \pm 0.419	-1.041 \pm 0.789	0.186 \pm 0.571	0.106 \pm 0.580	0.546 \pm 0.538	-1.265 \pm 0.221	0.416 \pm 0.204
	<i>Predicted</i> 95% <i>CI</i> ***	(-3.374, -1.702)	(-2.840, 0.404)	(-0.941, 1.343)	(-1.046, 1.276)	(-0.490, 1.656)	(-1.698, -0.832)	(0.0154, 0.817)
30 - m	<i>Mean</i> \pm <i>SE</i> *	0.02 \pm 0.01	0.00 \pm 0.00	0.09 \pm 0.03	0.02 \pm 0.01	0.06 \pm 0.02	0.19 \pm 0.05	0.55 \pm 0.07
	<i>Coefficient</i> \pm <i>SE</i> **	-3.880 \pm 0.642	-16.687 \pm 1603.687	1.505 \pm 0.720	-0.245 \pm 0.967	1.110 \pm 0.748	-1.555 \pm 0.249	0.113 \pm 0.222
	<i>Predicted</i> 95% <i>CI</i> ***	(-5.456, -2.829)	(0.000, 100.139)	(0.233, 3.177)	(-2.355, 1.714)	(-0.249, 2.818)	(-2.044, -1.066)	(-0.323, 0.549)

* Observed proportions of released *L. sylvaticus* reaching each tracking station (10-, 20-, 30-m).

** Treatment (2010): Untransformed logit coefficients \pm SE are those of the TREATMENT effects from the best (ANOVA *F*-test) quasi-binomial generalized linear model (GLM) fitted for each tracking distance. Reference treatment (2008-09): Untransformed logit coefficients \pm SE are those of the fixed effects from the best (lowest AIC) mixed effects binomial model (GLME; see A021-059-A1 in Popescu and Hunter 2011).

*** 95% confidence intervals for the predicted logit coefficients (GLM for 2010; GLME for 2008-09).

**APPENDIX B: QUANTITATIVE INDEX OF THE PERMEABILITY OF FIVE
OPEN-CANOPY VEGETATION TYPES TO JUVENILE MOVEMENTS
OF *LITHOBATES SYLVATICUS* DURING THE
POST-METAMORPHIC PERIOD**

This appendix describes a quantitative index of the permeability of our five open-canopy vegetation types to juvenile movements of *Lithobates sylvaticus* during the post-metamorphic period in 2010, with mature forest as a control (permeability = 1.0). Forest reference data were derived from the same experimental design and species in the same locale, using forest vegetation tested in 2008-09 (see Appendix 1 in Popescu and Hunter, 2011; Ecological Archives A021-059-A1). We assumed that juvenile wood frog movements would be facilitated (i.e., have highest permeability values) through mature forest (i.e., vegetation similar to the species' terrestrial settling habitat) and thus used mature forest as benchmark of permeability (index = 1.0). The index values for open-cover vegetation were (lowest to highest permeability): **1.** row crop (0.40); **2.** hayfield (0.47); **3.** forest clearcut (0.55); **4.** open-lawn (0.58); and **5.** moderate-cover lawn (0.67; see Table B.1 below).

Our composite index of permeability was based on four movement metrics: (1) the proportion of frog tracks at the last station (30- or 40- m); (2) the proportion of animals captured in the last runway section; (3) movement timing; and (4) movement rate. The first two metrics indicate an individual's *willingness to enter* a given treatment; the third and fourth metrics are estimates of *velocity* within that cover type. Without a strong sense of which of these metrics was the best measure of permeability, we opted for the simple default decision of giving equal weight to each. All individual metrics were

scaled to the highest value observed in that category prior to calculating our overall index. In only one case (metric #4, velocity) was an individual metric in the forest exceeded in absolute value by another treatment (i.e., velocity was greater in the open-lawn, moderate-cover lawn, forest clearcut, and corn field than in the mature forest treatment; see row 7 for *velocity* in Table B.1, below).

For metric #1 (proportion tracked out of total released), we used the values from the final tracking station (i.e., 30 m for 2010; 40 m for forest) (highest value was for forest: 0.50 proportion tracked at the final station). For metric #2 (proportion recaptured out of total released), we used the pitfall data from the distal compartments (i.e., 30-35 m for 2010; 40-45 m for forest). For metric #3 we identified the stations at which the greatest proportion of released animals moved on day 1, 2, and 3 post-release and averaged their values (highest value was for forest, where the greatest proportion of released animals were observed at the greatest distance: 0.75 proportion of the 40-m runway length). Velocity values (metric #4) were scaled to the highest value observed (i.e., 55.6 m/d in the open-lawn). Finally, we computed the average of all metrics for each treatment. The resulting index was expressed as a proportion of the benchmark forest value with an assumed permeability of 1.0 (as expected, the highest absolute permeability value prior to scaling was for mature forest: 0.83).

Our study provides a repeatable assessment of permeability at the scale of individual cover types, and the applicability of our results for conservation biology and management could be enhanced with our proposed quantitative permeability index. Specifically, it is plausible that our index could be used to parameterize demographic models of individual movement for juvenile *L. sylvaticus* (and potentially, similar

species) during dispersal in open-cover vegetation or fragmented landscape settings. However, we urge caution in the widespread application of this index to other study species or regions without careful consideration. For example, we only estimated permeability for one type of row crop (feed corn), and it is possible that juvenile movements would differ in other agricultural cover types or seasons, for other species, or as the dispersal period progresses and individual behavior changes. Further, our four movement metrics were weighted equally in the overall index of permeability, yet it is possible that in a biological sense each factor contributes differently to permeability as experienced by the frogs. Future studies or applications could consider alternate weighting scenarios that reflect a more nuanced understanding of permeability.

Table B.1. Composite quantitative index of the permeability of five open-canopy vegetation types to juvenile movements of *L. sylvaticus*, with mature forest as a control (permeability = 1.0).

Movement Metrics	Reference Treatment (2008-09)	Treatment (2010)				
	Mature forest*	Lawn (45-85% cover)	Open-lawn (0% cover)	Clearcut	Hayfield	Row crop (corn)
1. Proportion tracks out of total released final station (30 or 40 m)	1.00	0.12	0.04	0.04	0.00	0.18
2. Proportion recaptures out of total released end of runway (30-35 or 40-45 m)	1.00	0.80	0.33	0.67	0.97	0.23
3. Movement Timing** station at which largest proportion moved						
day 1	0.25	0.25	0.50	0.25	0.25	0.25
day 2	1.00	0.25	0.25	0.50	0.50	0.25
day 3	1.00	0.25	0.50	0.50	0.25	0.50
average of days 1-3	0.75	0.25	0.42	0.42	0.33	0.33
days 1-3 (scaled to forest = 1.0)	1.00	0.33	0.56	0.56	0.44	0.44
4. Velocity	0.31***	0.97	1.00	0.55	0.16	0.48
Overall Permeability Index (Unscaled)	0.83	0.56	0.48	0.45	0.39	0.33
Overall Permeability Index Scaled to Forest = 1.0	1.00	0.67	0.58	0.54	0.47	0.40
Order of Permeability (5 = highest; 1 = lowest)	Reference (1.0)	5	4	3	2	1

* Mature forest values are based on Popescu and Hunter 2011 (also see *Ecological Archives* A021-059-A1).

** The station distance at which the largest proportion of animals were moving on day 1, 2, and 3 following an experimental release expressed as a portion of runway length (e.g., 15 m station in 30 m runway = 0.5). Values were averaged across the three days then scaled to 1.0 for forest.

*** The only case when an individual metric in the forest was exceeded in absolute value by other treatments.

**APPENDIX C: MOVEMENT METRICS FOR FROGS (*LITHOBATES*
SYLVATICUS) RELEASED AND RELOCATED IN
DISTANCE-TO-FOREST EXPERIMENT
IN LAWNS AND HAYFIELDS**

Table C.1. Movement metrics for frogs released and relocated in distance-to-forest experiments in lawns and hayfields across six sites and four trials.

Treatment		# Released	# observed at path end	% net movements > 1 m	% net movements < 1 m	Net displacement (m)	Range: Net displacement (m)
Trial	Transect					Mean \pm SE	Mean \pm SE
Lawn		84 (total)	62	34.5	65.5	2.18 \pm 0.42**	0.00 - 19.95
Trial 1	(31 Jul)	21	14	23.8	76.2	1.31 \pm 0.63	0.00 - 13.62
Trial 2	(1 Aug)	21	17	57.1	42.9	4.09 \pm 1.05	0.05 - 19.95
Trial 3	(2 Aug)	21	14	42.9	57.1	2.87 \pm 1.02	0.00 - 19.80
Trial 4	(3 Aug)	21	17	14.3	85.7	0.46 \pm 0.10	0.00 - 1.72
	Transect 1 (30 ⁰)	28	21	39.3	60.7	1.73 \pm 0.45	0.00 - 8.60
	Transect 2 (45 ⁰)	28	20	35.7	64.3	2.75 \pm 0.90	0.00 - 19.80
	Transect 3 (60 ⁰)	28	21	28.6	71.4	2.07 \pm 0.77	0.00 - 19.95
Hayfield		84 (total)	62	13.1	86.9	0.73 \pm 0.20**	0.00 - 14.88
Trial 1	(31 Jul)	21	10	42.9	57.1	1.96 \pm 0.74	0.08 - 14.88
Trial 2	(1 Aug)	21	20	0.0	100.0	0.19 \pm 0.04	0.01 - 0.86
Trial 3	(2 Aug)	21	19	0.0	100.0	0.17 \pm 0.04	0.00 - 0.60
Trial 4	(3 Aug)	21	13	9.5	90.5	0.62 \pm 0.18	0.05 - 3.83
	Transect 1 (30 ⁰)	28	21	17.9	82.1	1.27 \pm 0.58	0.00 - 14.88
	Transect 2 (45 ⁰)	28	21	3.6	96.4	0.31 \pm 0.06	0.00 - 1.28
	Transect 3 (60 ⁰)	28	20	17.9	82.1	0.62 \pm 0.17	0.00 - 4.51
Total		168	124	23.8	76.2	1.46 \pm 0.24	0.00 - 19.95

Notes: Net displacement (m) by transect and frog start location are shown in Appendix D. All metrics above are based on net displacement (initial start to final location) and not total path length, and thus constitute conservative estimates of individual movements. Frogs observed at path end represents the number of juveniles relocated visually at conclusion of experiments.

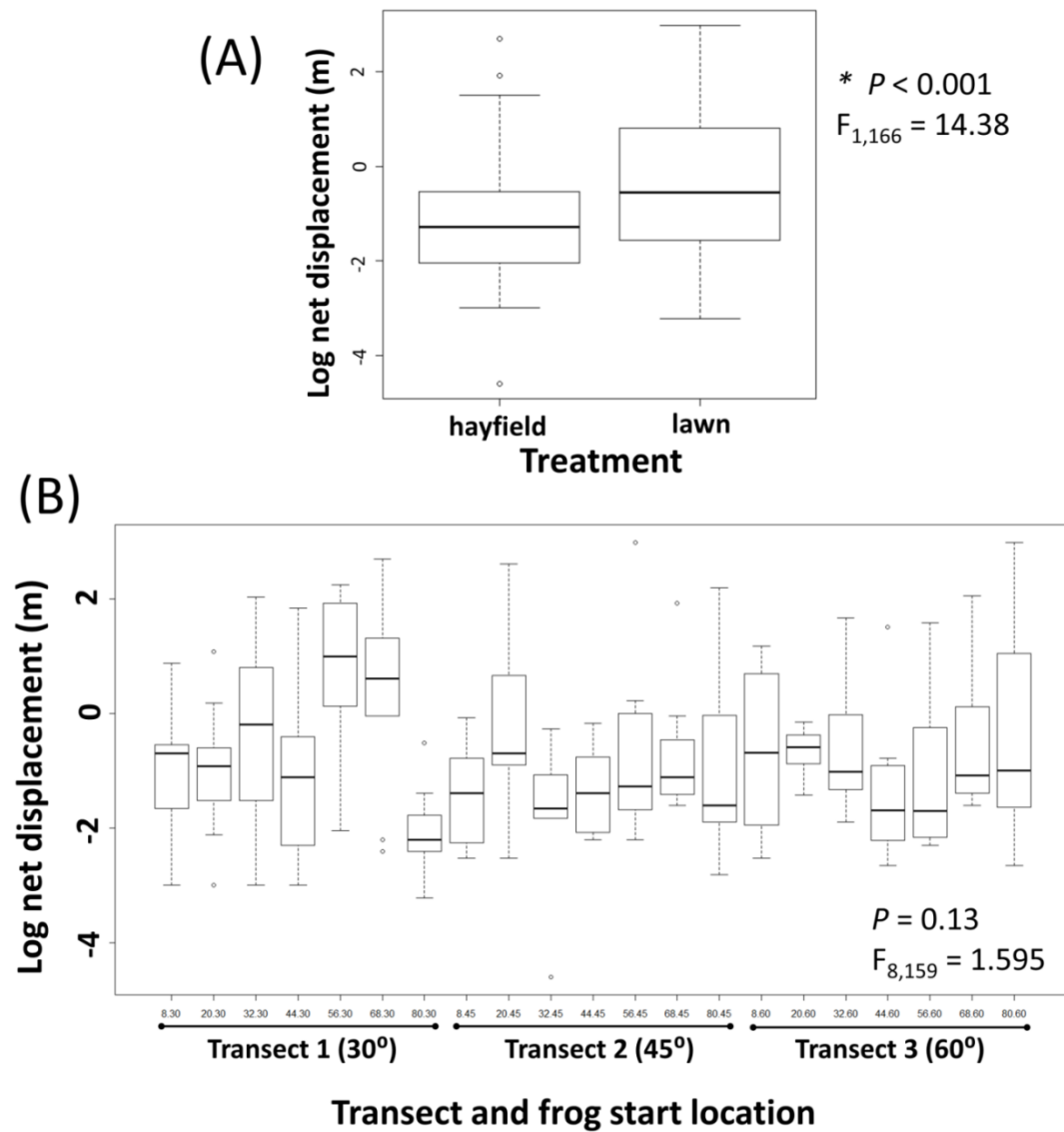
** Net displacement varied significantly by treatment (ANOVA; $F_{1, 166} = 14.38$; $P < 0.0001$).

**APPENDIX D: OBSERVED NET DISPLACEMENT OF *LITHOBATES*
SYLVATICUS RELEASED ALONG THREE TRANSECTS
EMANATING (30°, 45°, AND 60°, RESPECTIVELY) FROM
FOREST CORNERS IN TWO TREATMENTS
(LAWNS; HAYFIELDS)**

Observed net displacement (m) of *L. sylvaticus* (n = 168) released along three transects emanating (30°, 45°, and 60°, respectively) from forest corners (i.e., ~ 90° interface of contiguous forest and open-canopy vegetation) in two treatments (lawns; hayfields).

Panel (A) depicts effect of treatment on net displacement; panel (B) illustrates the effects of start location along each transect (8, 20, 32, 44, 56, 68, and 80 m from corner) (log-transformed to achieve normality).

Figure D.1. Observed net displacement (m) of *L. sylvaticus* (n = 168) released along three transects emanating (30° , 45° , and 60° , respectively) from forest corners (i.e., 90° interface of contiguous forest and open-canopy vegetation) in two treatments (lawns; hayfields).



APPENDIX E: ORIENTATION OF JUVENILE *LITHOBATES SYLVATICUS*
RELEASED ALONG THREE TRANSECTS EMANATING FROM
FOREST CORNERS AT TWO DISTANCE CLASSES

Orientation of juveniles (*L. sylvaticus*) released along three transects emanating from forest corners at two distance classes (**Class 1**: 8m, 20m, 32 m, 44m; and **Class 2**: 56m, 68m, 80m) in: (A) lawn; (B) hayfield. Bold solid lines in rose diagrams indicate the mean direction of frogs released on that transect; the length of the wedges represents the percentage of animals (5% increments) with orientations that fell within the designated 20° bin. Orientations were standardized so that 0° and 90° represent the two forest edges adjacent to treatments. Asterisks indicate transects and distance classes at which frogs demonstrated statistically significant directionality (Rayleigh Test of Uniformity or V-test); see Table 3.2.

Figure E.1. Orientation of juvenile *L. sylvaticus* released along three transects emanating from forest corners at two distance classes (Class 1: 8m, 20m, 32m, and 44m; and Class 2: 56m, 68m, and 80m) in (A) lawn; and (B) hayfield.

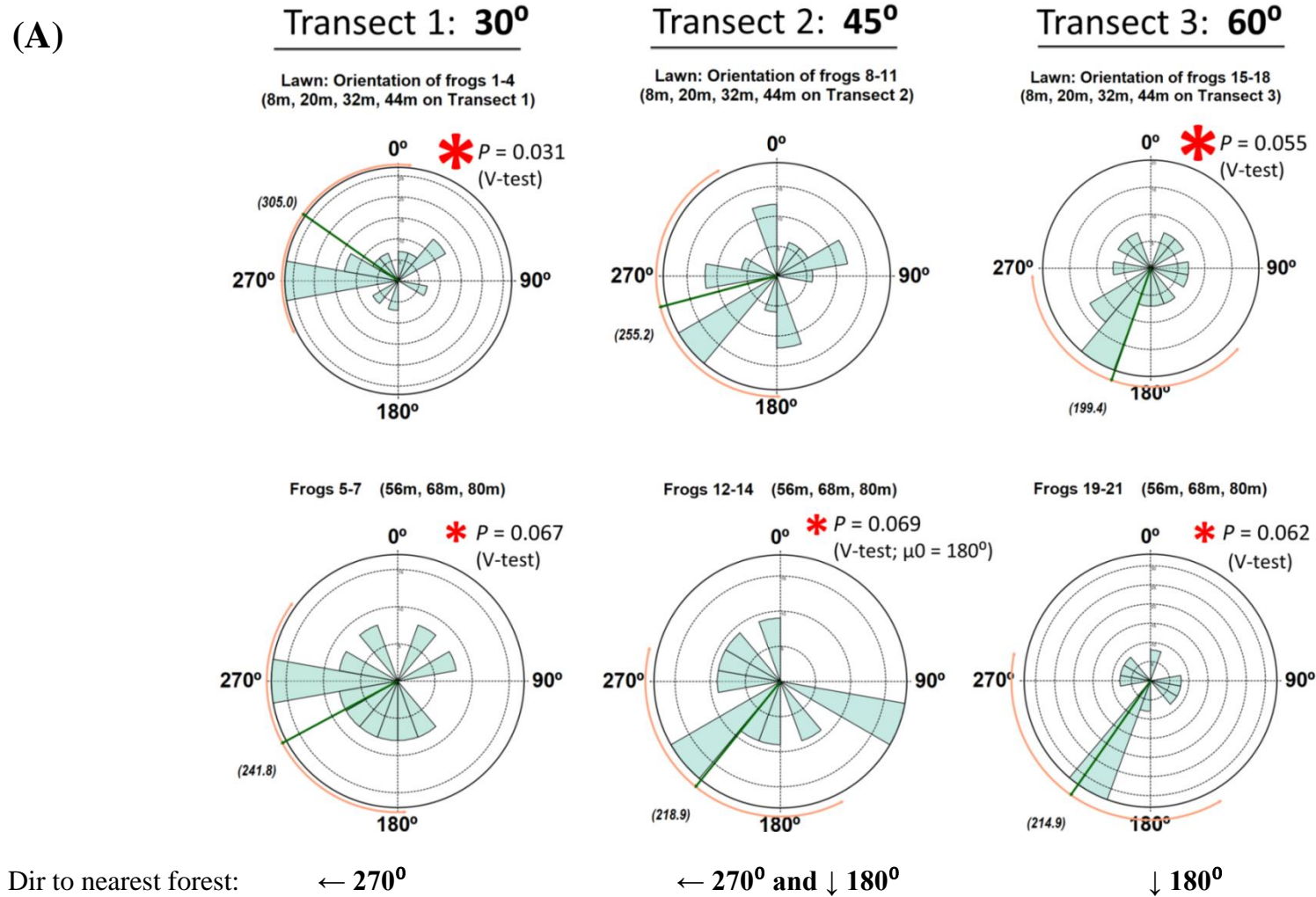
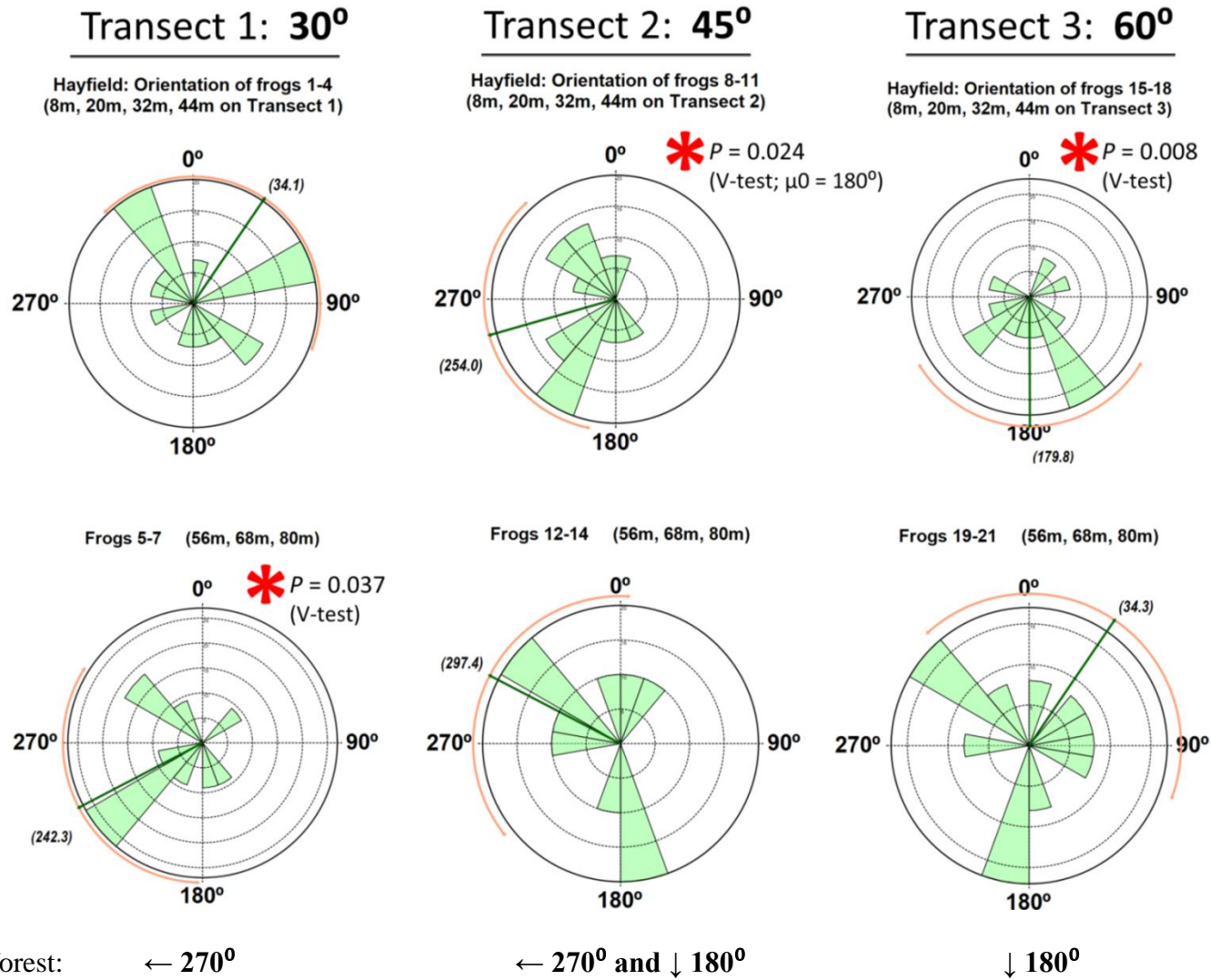


Figure E.1. (continued)

(B)



BIOGRAPHY OF THE AUTHOR

Brittany Blue Cline was born in Fort Collins, Colorado on 14 June 1979. She was raised in Newburgh and Raymond, Maine, and graduated salutatorian from Windham High School in 1997. She received her Bachelor of Arts degree in Biology and Environmental Sciences from Bowdoin College, Brunswick, ME in 2001. After undergraduate studies, she worked as land steward at Maine Coast Heritage Land Trust, and then as research assistant on a variety of biological conservation projects, spanning the gamut from species conservation to education and outreach. Some of her experiences included fall-migration passerine banding in North and Central America, avian disease and endangered species' restoration in HI, movement ecology of White-crowned Pigeons in FL, and nesting ecology of Black Oystercatchers in AK.

In 2008, Britt received her Master of Science degree in Fisheries and Wildlife from Oregon State University, Corvallis, OR. For her Master's thesis, she worked with Dr. Susan Haig to investigate the seasonal movement patterns of Wilson's snipe (*Gallinago delicata*) in agricultural wetlands of the Willamette Valley, OR. During 2009-2010, she worked as a wildlife biologist for USGS Forest and Rangeland Ecosystem Sciences Center on a project to investigate climate change impacts on semi-arid wetland systems in the western Great Basin (OR, WA, CA, UT). She was awarded the 2009 Distinguished Master's Thesis Award at Oregon State University.

Britt entered the Department of Wildlife Ecology at the University of Maine in 2010 to work with Dr. Mac Hunter on the effects of forestry, urbanization, and agriculture on the movement and dispersal ecology of juvenile amphibians. She received a graduate research fellowship with the National Science Foundation's Sustainability

Solutions Initiative at the University of Maine (2010-2014). She was recognized by the University of Maine Graduate School with 1st place finish in the Graduate Deans' Award for Mentoring Undergraduates in Research in 2014. After receiving her degree, Britt will join the University of Maine as a postdoctoral researcher to work on individual-based modeling of juvenile frog movements and dispersal. She will also serve as an undergraduate advisor and instructor in conservation biology. Britt is a candidate for the Doctor of Philosophy degree in Wildlife Ecology from the University of Maine in August 2014.